

**THE ECOLOGY OF THE BLACK-HEADED
HONEYEATER *MELITHREPTUS AFFINIS* IN
TASMANIA, AUSTRALIA.**

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Submitted in fulfilment of the requirements for the degree Doctor
of Philosophy, School of Zoology, University of Tasmania

June 2005.

This thesis contains no material, which has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

Kerryn Herman

Date

17/6/05

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ABSTRACT

The island state of Tasmania supports an environment unlike anywhere else in the country. Historically the land has been exposed to glacial conditions, been both isolated and attached to the rest of the continent. This has resulted in a unique array of flora and fauna. Of the birds species found in the state, 12 are endemic, and it is one of these species that is the focus of this study.

Melithreptus affinis is one of two members of this genus found in Tasmania, both of which are endemic. It was first described in 1835, and although known to science, little if any research has been undertaken on any aspect of this species ecology. This study rectifies this.

In a context of the Tasmanian environment, the foraging and time budget of *M. affinis* was constructed. Literature has already shown that there are significant morphological differences between *M. affinis* and the mainland *M. lunatus*, species believed to be allopatric counterparts. In fact, within the genus, both the Tasmanian species show much greater morphological divergence than the mainland species.

Results showed that *M. affinis* used a wider variety of habitats, or increased niche during this study, with foraging effort being distributed between gleaning and probing methods. These variations were influenced by seasonal factors and climatic conditions, showing the adaptability of the study species, and how closely it has evolved with the Tasmanian environment. Versatility was demonstrated when environmental conditions were less than optimal. Continuing this broadening of niche is the species use of a wider array of microhabitats than records show for Melithreptids on the mainland. Microhabitat use was distributed between upper, mid and lower canopies, whilst this genus is generally considered and upper canopy specialists. Again these changes may be a response to the climatic conditions at the time of the study.

To date the literature on the breeding biology of insular species is limited to a small body pertaining to Northern Hemisphere species. Characteristics such as lower clutch sizes, later laying dates, prolonged nestling development and increased adult survival have been attributed to island populations. This study

on *M. affinis* was undertaken to determine if such trends were consistent in a Tasmanian context. Analysis of both field data and museum specimens showed that there were no discernable differences in most aspects of reproduction. The characteristics shown by *M. affinis* are consistent with other members of the genus, as well as other members of the Meliphagidae family, except the duration of the incubation period in the species. This period is longer than would be predicted based on other members of the family. It is hypothesised that this increase may be the result of a longer history of this species in Tasmania and thus an adaptation to the colder conditions experienced during the glacial periods. It is not possible to compare this characteristic with the other endemic species, as this information is not available.

The lack of variation in the reproductive traits of this endemic species allows for this species to be considered equivalent to continental species, and raises the question as to the validity of insular or island effects on other aspects of the species ecology. This species has evolved in isolation, in an environment that has undergone substantial geological alteration, and has evolved in response to these environmental conditions.

ACKNOWLEDGEMENTS

There are many people who I need to acknowledge in regards to this study.

Firstly, I should thank my Mum who made me accept the offer of a PhD and stipend, even when I had my doubts about moving to Tasmania. Without her I would never have undertaken the task.

I would like to thank my supervisor Dr Randy Rose for his direction, support and editorial skills. I would also like to thank other members of the School of Zoology - Dr Mark Hindell for his statistical direction and Dr Alistair Richardson for comments made on chapter 2.

There are a number of people outside of the University who provided assistance with museum specimens:

- Ian Mason and Robert Palmer at the Australian Natural Wildlife Collection, CSIRO Sustainable Ecosystems, Canberra;
- Tammy Gordon at Queen Victoria Museum and Art Gallery, Launceston;
- Wayne Longmore and Rory at the Victorian Museum; and
- Walter Boles at the Australian Museum.

I need to thank Alan Fletcher for his assistance in mist netting and banding attempts. Many an hour was spent without results. This thanks extends to Sarah, Al and Phil who volunteered their time and energy in erecting and dismantling nets. Also Eli Widolf who monitored nest one season whilst I was interstate.

Thanks to the various postgraduate and honours students with whom I have spent both professional and personal time with over the last 4 – ish years; Fabienne who is back in France, Corrine who is in England, Alex who is somewhere in Victoria, Maria who is back in Greece, Bonnie in Newcastle, Abe who had to go back to Texas and Gab, who is the only one who has managed to stick around.

I need to thank Edwina who has been the only consistent person in my life for the past three years, and who has let me ramble on about a topic that only I seem to find interesting. Also thanks to Errol who has played a similar role, only via e-mail.

I need to acknowledge the 2002-2003 executive of Tasmanian University Postgraduate Association (TUPA), an organization I have been involved with for the duration of my candidature.

There are probably others that I haven't listed, but they are not forgotten or unappreciated. Without professional or personal support this thesis would not have been completed.

It is late and I am tired.

K.

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1. INTRODUCTION

In 1966, Ridpath and Moreau published a major paper on the ecology and evolution of the avifauna of Tasmania. Since this publication, surprisingly little research has been undertaken on the development of the avifauna, though our understanding of both the floristics and climate at the time of invasion continues to grow. In 1974, Thomas took the ideas of Ridpath and Moreau and developed them in the context of current literature, in an attempt to more conclusively explain speciation and diversity in Tasmania's avifauna. What Thomas' exploration did was pose more questions than it answered, and he concluded that until more was known about the life history strategies of Tasmania's birds and how they were connected with the ecological factors of Tasmania itself, a comprehensive hypothesis that dealt with both species impoverishment and high levels of endemism in Tasmania birds would be unachievable. Thomas (1974) states in his paper that any hypothesis he has developed needs further substantiation by observational data. It is the main aim of this thesis to provide the necessary life history data and ecological needs of one of Tasmania's endemic honeyeater species – *Melithreptus affinis* – to contribute to the theories pertaining to the evolution of Tasmania's current avian assemblage.

Two major factors have been used to develop hypothesis to explain both species paucity and high endemism in the avifauna of Tasmania. These are the effects of island biogeography and insularity (Thomas 1974, Abbott 1973; 1976; 1978, Abbott and Black 1981), and the past processes of climatic and geological change (Ridpath and Moreau 1966).

1.1 Theories of Island Biogeography

In 1967 MacArthur and Wilson published a text, putting forward a model to explain the variation found between populations of organisms on islands and mainland environments. The theory's original purpose was to explain the variation in species richness of an 'archipelago scale during ecological time' (Lomomlino 2000). This allowed the implications of evolution to be removed

from the model. Furthermore, the model assumed that only physical features of an island influenced immigration and extinction, ie: all species were equivalent in their ability to colonize and maintain their populations on an island (Lomolino 2000).

The theory states that the number of species on an island is the result of a dynamic interplay between immigration and extinction, with species numbers tending towards an “equilibrium” (Gilbert 1980). This equilibrium occurs as a result of the rate of immigration being balanced by the rate of extinction, with the rates being determined only by island area and isolation (MacArthur & Wilson 1967). There is an underlying assumption to the theory that suitable islands are isolated from one another by hostile habitats.

The “Theory of Island Biogeography” (previously referred to as ‘Species equilibrium’) developed by these authors stood for a long time as a paradigm in the search for answers to explain the phenomenon of insular variation.

Since the inception of the theory, contemporary scientists have argued support of and objection to this universal, though simplistic representation of what is essentially a very complex issue. For a long time, there was almost complete agreement, with many studies dismissing their own results if they did not fit with the predicted model (Cox & Moone 1993). This lack of fit in itself should have been considered significant, if for no other reason that it did not fit the model. However, the majority of biogeographers accepted these as ‘exceptions which prove the rule’, rather than fundamental challenges to the theory (Brown & Lomolino 2000).

Whether MacArthur's and Wilson's (1967) theory is reflective of reality or not, its legacy – the increase in research on the interaction of island biotas – has been substantial. Whittaker (2000) suggests that the theory be considered equal to other models, and that modern island biogeographers no longer give primacy to equilibrium models as a matter of faith (pp 83). He raises issues with the questions historically asked and the landscape scale on which these are trying to be answered; indicating that if these problems are resolved then a greater understanding of island biogeographical patterns may be obtained.

A decade after the publication of MacArthur and Wilson's theory, Lack (1976) published a book specifically on terrestrial island avifaunas. This had been preceded by a paper in 1970 on island birds. The conclusions reached by Lack (1970; 1976) differ substantially from those of MacArthur and Wilson (1963; 1967). Whilst MacArthur and Wilson postulate a dynamic theory, where there is a consistent turnover of species, and equilibrium between extinction and immigration, Lack (1970; 1976) suggested that, at least within avifauna, species numbers are constrained by a number of ecological variables, predicting relative stability in terrestrial island avifaunas. For this group of organisms (terrestrial birds), dispersal is not a largely hindering factor, with distances between mainland and islands not being beyond the flying capacity of many species. Thus isolation is not a primary factor affecting land birds (Lack 1976). However, islands continue to support a depauperate avian community compared to mainland areas. Lack (1970) suggested three factors that may account for the decreased species diversity:

- an (as yet) undetected ecological requirement;
- lack of "ecological room"- conditions may suit in the short term, but not the long term, leading to extinctions; and/or
- broader niches of island species, which replace two or more specialized species.

Rapid invasion occurring as a result of anthropogenic disturbance, gives credit to Lack's theory of ecological constraints. By changing the environmental conditions and creating greater habitat variability, thus removing some environmental constraints, it allows species of birds that were physically able to reach isolated islands, but unable to establish viable populations, to invade and establish themselves. Abbott (1983) supports the viewpoint that an island's habitat needs to be 'opened up' to allow colonization; attributing much of the species turnover in birds and mammals on islands off the west coast of Australia as a result of human impacts. Walter (1998) drew similar conclusions when considering avian species turnover in the Revillagigedo archipelago, in the eastern Pacific Ocean. His results suggested that a shift away from the equilibrium model is necessary in modern conservation

science, and highlighted the occurrence of 'novel niche' spaces as a result of human impact, allowing colonization by species that had previously been unrecorded in the archipelago.

Lack's (1970; 1976) ideas on island biogeography are also not without their critics. The major issue with the theory is that it suggests a static view of species composition; that species numbers are maintained about a figure, which is determined by a fixed number of available niches (Thornton *et al.* 1993). This rigidity in species composition and turnover should only be applied in the absence of major disturbances (Whittaker 2000), indicating that a stable environment allows for stability in the species able to inhabit it. Island habitats are hypothesized to be less seasonal or variable than mainland habitats, which result in more predictable resources (Cody 1966; Macarthur & Wilson 1967; Blondel *et al.* 1992), thus providing a more stable environment, allowing, as suggested by Lack (1976), and supported by Abbott (1983) and Walter (1998), stability in the avian species present in island biotas.

Both Macarthur's and Wilson's and Lack's theories of island biogeography have been applied to the Australian continent and surrounding islands – including Tasmania. Abbott (1973; '74a; b; c; '76; '77; '78; '80; '81) has undertaken much of the research on this aspect of Australian avifauna, with a contribution by Keast (1968a; 1970; 1976a; 1976b).

Conversely to the theories developed in the Northern Hemisphere, Abbott (1978) found that the landbirds of Australian islands were more stable, and less prone to extinction. Subsequently, he rejected the Equilibrium Theory of Island Biogeography. For both the islands off the southwest of the Australian continent and of Bass Strait, a level of stability was encountered, with Abbott (1973; 1978) concluding that the main factor influencing the diversity of species on these off shore islands was the habitat structure and subsequent resource availability (Abbott 1976), and the inability of most species to cross the tracts of water necessary for colonising island environments. Those species that have been able to colonise Australian islands over the last 150 years have been introduced by man (Abbott 1978).

Woinarski, *et al.* (2001) believe that environmental variability is clearly an important factor in determining the richness of bird species on islands, but it remains a far more nebulous concept than the more readily measured variables of island size, isolation or topography.

Thomas (1974) believed that the Macarthur and Wilson theory of Island biogeography provided an adequate explanation for the avian diversity in Tasmania. He dismissed Abbott's suggestion of a barrier effect from Bass Strait, suggesting that isolation (or lack of) does influence the species turnover, and that island area (and the implications of increased habitat heterogeneity with increased island area) is the major factor in the total Tasmanian avian diversity (Thomas 1974). Thomas also stated that the Tasmanian avifauna is impoverished, but saturated, and has reached a dynamic state of equilibrium (Thomas 1974 pp 346) in line with the Macarthur and Wilson model.

1.2 Palaeobotanical evidence and the invasion of Tasmania's avifauna.

1.2.1 Vicariant events and speciation

Neither Abbott nor Thomas placed much emphasis on the Tasmanian environment, or take into consideration the geological history of the island in their development of speciation theories. Tasmania has been exposed to unique geological conditions. It is the only area of the continent to undergo extensive glaciation during the Pleistocene epoch (Williams 1974), and although presently separated from the mainland by Bass Strait, at times in history, this Strait was bridged (possibly 3-4 times over one million years), allowing for movement into and out of the region. In essence, the Strait has acted as both a biological barrier and a filter, causing both a biogeographical and ecological effect (Williams 1974). Also Tasmania is considered to have a cool temperate maritime climate, which causes conditions of more equable temperature range than continental Australia, with higher, more even rainfall encountered across the state (Williams 1974).

These features have led to the evolution of a unique biota, in some instances relictual (for example *Nothafagus sp.* in temperate rainforest), which must have implications for the avian species diversity of Tasmania. These physical attributes have an impact on which species of birds are able to invade the Tasmanian land mass, when these species have invaded and how successful they have been. The question is how do these attributes affect the avifauna. Area and isolation (Macarthur and Wilson's theory of island biogeography), and habitat variation and stability (Lack) undoubtedly influence the species diversity of land birds found in Tasmania, but these factors taken alone are not enough to adequately explain Tasmania's avifaunal assemblage.

Evolutionary ecologists have long been trying to explain the processes by which the current biota's have developed across the world. Speciation usually proceeds when populations become isolated (Ford 1987a), with two kinds of speciation being recognised – those that are isolated by geographical barriers into numerous relatively large populations (vicariant mechanism), and those whereby small, peripheral populations become isolated from the main population, either by individuals establishing a colony beyond the range of the main population, or by a remnant being stranded as a result of climatically unstable period (parapatric variation) (Ford 1987b). The mechanisms by which Australian avifauna evolved have been tested on numerous occasions, without any conclusions yet being substantiated.

Broadly speaking, Australia is comprised of a series of relatively mesic areas of endemism, located around the periphery of the continent, with a smaller number of arid areas of endemism located within the interior (figure 2.1, Cracraft 1986). These areas are well established (Keast 1961; Ford 1987a; Ford 1987b; Cracraft 1991), and biogeographical trends are consistent across not only avifauna, but other vertebrate groups (Cracraft 1991) (fig. 2.1).

In 1986 Cracraft suggested that two major vicariant elements have strongly influenced the evolution of Australia's vertebrates. He suggests these are geomorphological barriers or climatic-ecological barriers, both of which segregate widespread biotas into smaller entities, allowing for the creation of areas of endemism, such as Tasmania. The geomorphological barrier theory, however, which suggests that long distance dispersal across pre-existing

barriers (for eg. Bass Strait) is the most common mode of speciation, is not consistent with speciation patterns examined for the Australian continent (including Tasmania), thus suggesting that climatic-ecological barriers may be more important.

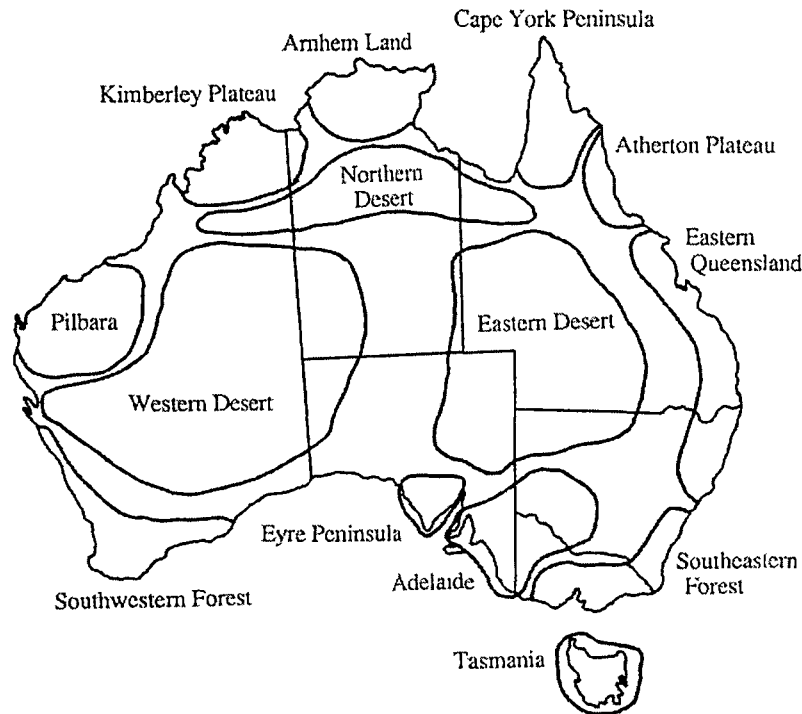


Figure 2.1 Areas of biotic endemism across the Australian continent (from Cracraft 1991).

Subsequently, Cracraft published two more papers (1991; 1994) on the speciation of Australian avifauna. These both drew the same conclusion - that a single climatic-ecological vicariant pattern best explains all the data.

McLennan & Brooks (2002) re-analysed Cracraft's data using Brooks Parsimony Analysis (BPA), a statistical method suggested to be more sensitive to the different possible manifestations of geological dispersion (Brooks & McLennan 2001). Their analysis supported Cracraft's (1986) original conclusion that members of the Australian avifauna had been strongly influenced by two different vicariant elements. However, their re-analysis differed significantly from all Cracraft's previous work (1986; 1991; 1994)

suggesting that the Australian avian biota is a mosaic of vicariance, peripheral isolates, speciation, post-speciation dispersal, non-response to vicariance and extinction. Furthermore, the same areas often have reticulated histories with respect to the species that inhabit them (McLennan and Brooks 2002). Consequently, building a model of Tasmania's avifauna and its evolution is a complex matter, and the hypothesis suggested later in this chapter may only represent a small portion of what actually happened.

1.2.2 Biotic diversity in Australia

Four general themes have dominated the conception of biotic diversity in Australia. These have been developed generally from studies on taxonomically restricted groups of species with emphasis placed on singular events, rather than on the broader patterns that Cracraft (1986; 1991) and McLennan and Brooks (2002) have defined. These themes can be seen throughout the literature already reviewed. Broadly, as defined by Cracraft (1991) these themes are:

1. Australian biota has developed as a result of numerous waves of colonization and subsequent radiation;
2. Two major biota's were developed – arid interior and moist peripheral areas
3. Arid interior biota's arose via independent colonization from continental margins; and
4. Speciation events producing modern biota, especially in peripheral areas, are predominately Pleistocene in age.

The problems with these assumptions are outlined in Cracraft (1991) and are apparent when looking at the resultant cladograms of analysis on data sets (Cracraft 1991; 1994; McLennan & Brooks 2002). The groupings of endemic biota do not reflect the above assumptions for all fauna groups - not just birds. Biotic diversity in Australia is the result of much broader, more complex multiple events, with similarities in biota's occurring between areas of endemism (fig 2.1) not consistent with the broad themes applied.

The evidence about the importance of the Pleistocene in Tasmania's avifauna is limited, but suggests that this period has been most influential on the development, conversely to Cracraft's (1991) conjecture. Thomas (1978) found no modern bird species to be strongly associated with the Temperate Rainforests of Tasmania, a vegetation assemblage that predates the glacial periods of the Pleistocene (Hill *et al.* 1999). Also the major vicariant events known to impact upon Tasmania are those associated with the major glacial periods of the Pleistocene. During this geological period, the landmass known as Tasmania was attached to the continental mainland of Australia by the Bass Strait land bridge. Interglacial periods saw this land bridge recede as sea levels increased. The effects of climate change, vegetation change and isolation must all have played a part in the development of Tasmania's current avian assemblage.

1.3 Palaeoclimate and Palaeobotany in Australia

Changes in climatic and environmental conditions across the continent have influenced the movement and subsequent historical habitation of Tasmania by avifauna. The understanding of these changes has significantly increased over the last decade.

Palaeobotanical evidence now available has allowed scientists to further understand the environment of Tertiary Australia and how this changed in the Quaternary period. The implications of glacial periods, and climatic fluctuations as a result of these glacial events, continue to be elucidated, as do the changes in the climate when moving out of the last glacial period into the Holocene.

Tertiary Australia is believed to have supported a mesophytic flora (Keast 1961), with species such as *Nothofagus* dominant (Kershaw *et al.* 1991). Tasmania's flora has very substantial similarities to that of the southeast corner of Australia through this period (Hill *et al.* 1999). The climate is believed to have been humid and warm, allowing for the ascendancy of rainforest flora (Keast 1961; Hill *et al.* 1999). However, in Tasmania, other floral components were developing such as scleromorphic heath and alpine adapted vegetation. Vegetation changes start to become prominent towards

the end of the Eocene as the climate begins to deteriorate, with an increase in the drought and cold adaptations in plants (Hill *et al.* 1999). Evidence from mainland Australia and Tasmania suggests that as time progressed from the late Tertiary the climate became cooler, considerably drier and more seasonal than it had been during the early Tertiary. It is possible that during the middle Pliocene the climate may have become warmer and wetter, before the onset of the glacial periods and the major climatic shifts associated with the Pleistocene (Hill *et al.* 1999).

Unlike much of mainland Australia, Tasmania was substantially affected by glacial ice. During the most extensive glaciation of Tasmania, an icecap of ~ 6000km² developed across the central highlands (Kiernan 1990). This is believed to have occurred late in the Pliocene or early on in the Pleistocene. At least three subsequent glaciation events have occurred (Kiernan 1990). Glacial occurrence has had a much greater importance in Tasmania and on the development of its current environment than it has for other areas of Australia.

Climatically, current evidence suggests that during the Pleistocene, Australia was more partial to substantial fluctuations in both temperature and precipitation levels. Pollen samples provide the most conclusive evidence of climate change through the Pleistocene (Chappell 1991), with other evidence (such as geomorphology) strongly supporting the trends determined by botanical evidence.

Evidence suggests that during glacial periods, the climate was colder and substantially drier than during non-glacial periods (Hill *et al.* 1999). This is in contrast with previous beliefs that glacial climates were much wetter than interglacial periods (as suggested by Keast 1961 and Ridpath and Moreau 1966). Glacial climates were considerably colder than modern ones (by 5-8 degrees cooler), and tended to be drier. Interglacial climates were similar to those of the present day if not a little warmer and wetter. Evidence from early Pleistocene sites suggests that climate was considerably cooler and drier than current conditions that now occur in Tasmania (Hill *et al.* 1999).

The understanding of pollen records from the last interglacial-glacial cycle is extensive, with a continuous record of interglacial and glacial pollen records

from numerous sites across Western Tasmania (Colhoun 2000). What these records show is the fluctuation of vegetation, providing a clear picture of the palaeoenvironments during this time period (130-120k ybp). From analyses across a number of west Tasmanian sites, Colhoun (2000) has been able to construct a vegetational history of the area, one that is the most complete of any areas in the country. Pollen records indicate that during the interglacial period, the vegetation was dominated with cool temperate *Phyllocladus aspleniifolius* – *Nothofagus cunninghamii* rainforest. As temperatures decreased into glacial condition, the vegetation changed to alpine shrubland, or alpine grassland and herbland vegetation (Colhoun 2000). During the Glacial maximum, the pollen evidence suggests that most of western Tasmania was dominated by vegetation of alpine grassland and herbland vegetation, with areas of *Casuarina* and *Eucalyptus* woodland and rainforest taxa below 100masl on valley floors near the coast (Colhoun *et al.* 1999; Colhoun 2000).

Similar fluctuations have been observed in the vegetation of the Australian mainland. Desmarchelier *et al.* (2000), in an analysis of a late middle Pleistocene speleothem from South Australia again finds this fluctuation. During the interstadial period the vegetation was dominated by C3 plants as seen today, though conditions at this time were probably moister than now. Full glacial conditions, in contrast, appear to be associated with a sparse vegetation cover of predominately C3 grasses (Desmarchelier *et al.* 2000).

Pollen evidence from multiple sites in South-eastern Australia continues to show this fluctuation in vegetation types between glacial and interglacial periods (Kershaw *et al.* 1991). During the late Tertiary, close-canopied rainforest prevailed across the southeast of the continent, dominated by high levels of *Nothofagus*. This vegetation type begins to decline, to be replaced by members of Casuarinaceae and the coniferous Podocarpaceae (Kershaw *et al.* 1991). *Eucalyptus* types also show significant percentages in late Tertiary pollen samples. Moving into the early Pleistocene, pollen records are characterised by high levels of Casuarinaceae and Asteraceae. *Eucalyptus*, Poaceae and Chenopodiaceae values are relatively low, whilst rainforest taxa are almost non-existent in the samples. The most similar parallel to this in

modern vegetation is that of the alpine vegetation of southeastern Australia (Kershaw *et al.* 1991).

Mid Pleistocene pollen samples continue to be dominated by Casuarinaceae forest and woodland during the warm, wet interglacials. The dry cooler glacial periods are characterized by a high percent of herbaceous taxa, particularly grasses, indicative of very open vegetation. The variation in vegetation during the mid Pleistocene period was much greater than during the early period, perhaps reflecting a high magnitude of glacial/interglacial oscillation (Kershaw *et al.* 1991).

Late Pleistocene vegetation was similar to that of the early Holocene, with low levels of Casuarinaceae, significant levels of *Eucalyptus* and a high percent of Asteraceae, Poaceae and Chenopodiaceae during the last interglacial period. These vegetative assemblages are very different to those inferred from previous interglacial periods where Casuarinaceae dominated (Kershaw *et al.* 1991).

Further evidence is appearing with regards to the presence of scleromorphic vegetation present in Tasmania, pre-dating either human habitation, or the final (Margaret; Colhoun *et al.* 1989) glaciation. This is important in relation to the development of the current avifauna, particularly the endemics, and is a point that differs from past theories on Tasmanian speciation.

Located on the shores of Macquarie Harbour, western Tasmania, are the stumps of more than 365 trees and shrubs. These have been aged to pre-date the last glacial maximum, and are almost monospecific in genus. They have been identified as belonging to the genus *Melaleuca* (family Myrtaceae), probably *M. ericifolia* (Rowell *et al.* 2001), dominating a swamp forest. This discovery highlights the presence of scleromorphic vegetation during glacial periods, perhaps as remnants, but present all the same.

At the height of the last glacial maximum, sea levels were lowered, fusing the separate elements of 'greater Australia' into a single land mass (Luly 1993). This increased the total land area of continental Australia by nearly 30% (Dodson 1989), allowing for remnant coastal vegetation to survive during glacial restriction (Luly 1993). After the final glacial maximum, the climate

became warmer and moister during the early Holocene (Anker *et al.* 2001), and saw the reappearance of woodlands as a widespread element in the landscape (Luly 1993). Treeless vegetation was gradually replaced by woodland vegetation. In Tasmania, the early Holocene (13-6ka) brought closed *Nothofagus cunninghamii* forest development in the west and open *Eucalyptus* forest to Eastern Tasmanian (Jackson 1999). As the Holocene progressed, the climatic conditions became drier and cooler (Markgraf *et al.* 1986), with the development of the modern flora during this period (Jackson 1999; Anker *et al.* 2001).

Kirkpatrick and Fowler (1998) modelled likely glacial forest refugia in Tasmania. Their models suggest that during the last glacial, Eucalypt forest was relatively widespread around the coast of the state, covering approximately 14.9% of the land area (present area 19.8%). Rainforest/wet sclerophyll covered an area of approximately 7.2% (present 71.3%) and grassland/grassy woodland 32.5% (present 8.7%). The remaining 45.5% of glacial area was alpine vegetation (0.1% present)(Kirkpatrick & Fowler 1998). The eucalypt forest has not increased substantially between the last glacial maximum and present.

The botanical evidence provides a structure for the climatic and vegetational changes in Tasmanian during the Pleistocene. What it shows is an environment that fluctuated between warm, wet interglacial periods where temperate rainforest and *Casuarina* sclerophyll woodland dominated, to cold, dry glacial periods, where an open alpine grassland and herb land predominated across the landscape.

To correspond with this environmental change is the development of the Bass Strait land bridge. This was completely open during glacial periods, when alpine vegetation was at a maximum, and woodland/rainforest was confined to coastal refuges. At this time, areas of Tasmanian were covered in glacial ice, with temperatures 5-8 degrees cooler than modern day climates. After the glacial events, the climate became warmer and drier, allowing the development of modern day vegetation.

1.4 What does this mean for Tasmania's terrestrial avifauna?

The changes in the botanical evidence, as they are now understood, differ substantially from the conditions previously used to explain the invasion and subsequent speciation of Tasmania's current terrestrial avifauna. Climate fluctuations during the Pleistocene, the last time Tasmania was attached to the mainland, were cooler and drier during the glacial periods and warmer and wetter during interglacials.

Keast (1976b) suggested that resultant colder temperatures of glacial periods would have made Tasmania a less desirable habitat for birds, and hence it would seem likely that colonization occurred during melting phases (Interglacials) and as water-gaps were coming into existence. Ridpath and Moreau (1966) drew a similar conclusion. The difficulty with this hypothesis in light of the palaeobotanical evidence is that this time period corresponds with the expansion of 'desirable' habitat on mainland Australia.

During glacial periods, broad scale vegetational patterns are of widespread alpine and subalpine grasslands and herb land dominating the landscape. These replaced the woodland dominated by *Casuarina* sp. and temperate rainforests of *Nothofagus* common during the interglacials. As these more desirable habitats contracted to their coastal refuges (reflected in current day areas of endemism), those organisms dependent on this vegetation would be forced towards coastal areas. This constriction included the southeast of the Australian continent, with vegetation contracting towards the current Victorian coast. At the same time as appropriate habitat became sparser, the Bass Strait landbridge opened up, providing a relatively short distance for land birds to travel across to find other remnant vegetation. Pollen evidence indicates the tenacity of scleromorphic and *Eucalyptus* woodland in coastal and sheltered locations (Colhoun 2000), allowing for bird survival during the harsh climatic conditions.

The contraction and expansion of vegetation during the Pleistocene, combined with the opening and closing of Bass Strait provides a mechanism increasing the chance of woodland birds entering the Tasmanian landmass during periods of climatic hardship. This probably happened on multiple occasions

(Williams 1974), and is supported by Cracraft's (1991) evidence of multiple vicariant events resulting in the modern biota of Tasmania.

The vegetational changes during the glacial cycles as currently understood now provide a mechanism, increasing the chance of species crossing the landbridge and colonizing Tasmania. This is consistent with Keast (1976b) idea that species moved into Tasmania across Bass Strait when the land bridge was open. It may also help to explain why birds entered an area of such harsh climatic conditions.

For the non-endemic terrestrial species this invasion probably occurred during the later stages of the final glacial period, resulting in Tasmania's modern avifauna. Invasion during this period – when Tasmania was a part of continental Australia, may also account for the depauperate nature of Tasmania's terrestrial avifauna (Thomas 1974).

Both island biogeography theory (Thomas 1974) and ecological constraints (Abbott 1983) have been applied to explain the reduction in species diversity encountered in Tasmania. Table 2.1 provides a comparison of the Tasmanian avifauna with that of Victoria. Both hypotheses of species diversity are based on Tasmania being an island at the time of invasion. If invasion occurred across the landbridge, this raises the possibility of peninsular effects in a Tasmanian context (Thomas 1974).

Table 2.1 Comparison of the Tasmanian avifauna with that of Victoria. Figures in brackets exclude species living in habitats which do not occur in Tasmania. Adapted from Ridpath and Moreau (1966) and Thomas (1974).

| Group | Tasmania | | Victoria* | |
|-----------------------|-------------------|------------------|-------------------|------------------|
| | Number of Species | Percent of total | Number of Species | Percent of total |
| Water birds | 25 | 24 | 56 (37) | 19 (20) |
| Raptors and Owls | 11 | 11 | 23 (19) | 8 (11) |
| Game and Ground birds | 4 | 4 | 12 (5) | 4 (4) |
| Other non-passerines | 16 | 15 | 46 (25) | 16 (14) |
| Passerines | 48 | 46 | 148 (90) | 53 (51) |
| Total | 104 | 100 | 285 (176) | 100 (100) |

The peninsular effect is the phenomenon of a decrease in the diversity of organisms the further along a peninsular one progresses (Simpson 1964). A bottleneck forms in areas of narrow land, such as a land bridge, limiting the number of species able to pass along and subsequently colonize the peninsular. The rate of extinction along the peninsular increases compared to the adjacent mainland (Busack & Hedges 1984). This effect has been supported in rodents (Taylor & Regal 1978) but disputed in other faunal groups such as reptiles (Sieb 1980; Busack & Hedges 1984). Cook (1969) found that this effect occurs in birds in North America.

The decrease in the number of species able to cross the land bridge, combined with the climatic conditions in Tasmania at the time may have contributed to the reduced number of terrestrial birds species able to inhabit Tasmania. Those species able to adapt to the climatic conditions and fill niches otherwise vacant would have been able to persist in Tasmania, and should still be present in the modern avian assemblage.

In the case of the 12 endemic species, their history in Tasmania may be longer than for the non-endemic species. Ridpath and Moreau (1966) provide evidence for the persistence of one endemic species through the last glaciation, the Scrubtit *Acanthornis magnus*. Another species that may be considered relict, based on its ecological requirements, is the Forty-spotted Pardalote (*Pardalotus quadragintus*). This species is so specific in its requirements (Woinarski & Bulman 1985) that a long association with its environment would have been necessary for such development. The species is also highly sedentary, a trait very different from other pardalotes; perhaps the result of being confined to habitat remnants during glacial maximums.

Fossil evidence is available for one Tasmanian endemic that proves the species in its modern form was extant through out the Pleistocene. Remains of the Tasmanian Native Hen, *Gallinula mortierii*, have been found across a range of sites on the mainland, as far north as Chinchilla, Queensland (Baird 1984). These remains have been dated as being between 12 000 and 20 000 years old, being present during the final glacial maximum. This is a grazing species, dependent on short, lush pasture for feeding, and permanent water for breeding (Ridpath 1972). The vegetation changes during glacial periods

would have been conducive to this species, allowing the range to expand into the grasslands that dominated much of the continent during the glacial period. There is also evidence of extensive inland lakes across eastern Australia (Chappell 1991), providing necessary breeding requirements. From fossil evidence, Baird (1984) suggests that this species was distributed across all of Victoria, a large part of eastern South Australia, and the southern part of Queensland during the last glacial period. In the case of this species, the opposite effect is seen with the vegetational changes, that potentially during glacial peaks the distribution expanded, and the species contracted coming out of glacial periods as grasslands were replaced by sclerophyllous vegetation. If this species persisted during glacial periods it could be assumed that the species has cold climate adaptations. This may be why the species was able to continue as a remnant population in Tasmania, but not in other areas where temperature increases in recent times have been substantially greater. That one modern species was able to persist throughout the glacial periods is indicative that others may have survived the conditions also.

Lack of predation in Tasmania is also believed to have contributed to the survival of *G. mortierii*, with dingoes wiping out the population on the Australian mainland (Ford pers. comm.)

Further evidence of endemic species persistence between glacial events may be confirmed by the occurrence of multiple invasions. Keast (1970; 1976b) and Abbott (1973) both explore this concept. For a number of genera of terrestrial birds found in Tasmania, there is divergence between endemic species, and a congeneric species distributed across continental Australia (Table 2.2). The endemic species have generally shifted their niches in comparison to mainland counterparts allowing both species to co-inhabit.

Modern pollen evidence allows for the speculation that compatible habitat was present during the mid to late Pleistocene to allow bird colonization. The vegetational changes associated with glacial periods also provide a mechanism by which birds moved into Tasmania. This combined with fossil and ecological evidence of modern birds provides further indication that aspects of the terrestrial avifauna in Tasmania may have been able to colonize Tasmania earlier than previously thought.

| Endemic | Non-endemic |
|--------------------------------|---------------------|
| <i>Acanthiza ewingi</i> | <i>A. pusilla</i> |
| <i>Pardalotus quadragintus</i> | <i>P. punctatus</i> |
| <i>Sericornis humilis</i> | <i>S. frontalis</i> |
| <i>Melithreptus affinis</i> | <i>M. lunatus</i> * |
| <i>Platycercus caledonicus</i> | <i>P. elegans</i> * |

Table 2.2 Endemic and non-endemic species resulting from multiple invasions (From Keast 1970; 1976b and Abbott 1973) * indicates species recorded on Bass Strait Islands, but not inhabitant of the Tasmanian mainland.

It may be possible to infer the time of colonization of an endemic species based on ecological attributes. There is an extensive body of literature committed to exploring the variations between mainland species and their island counterparts. If a Tasmanian (and subsequently island) species shows divergence in characteristics from mainland co-generics it may be that this species has evolved in isolation, thus suggesting colonization occurred as Tasmania was becoming isolated from mainland Australia. If divergence does not occur, perhaps species invaded Tasmania when it was still a part of mainland Australia, making species now endemic to Tasmania equivalent to 'mainland' species.

1.5 Ecological and Morphological Variations

Much has been made of island species' abilities to colonise and successfully inhabit an environment different to that which mainland counterparts inhabit. This has led to theories of ecological release in island species, and subsequently niche expansion.

An organism's niche is the full range of physical and biological conditions under which it can survive and successfully reproduce (Liebold 1995). Ecological release is the expansion of the realized niche of a species where few competitors exist, but an undiminished range of resources and habitat are present (Cox & Ricklefs 1977). Insular avifaunas are well known to have lower species diversity than larger mainland areas (Wright 1980), the

implications of which have led to studies on the various ways insular species alter their 'niche' when interspecific interaction enforced elsewhere are removed. With these adaptive shifts in ecology, morphological traits also diverge (Keast 1961; 1976a).

One genus of birds, the *Parus* species (tits) has been studied extensively across much of the geographic range of the genus (Isenmann 1987; Veistola *et al.* 1995). Grant (1979) drew attention to morphological variation in the Canary Island Blue Tit (*Parus caeruleus*). He showed that the variations on the islands were not due to chance, but the result of the unique adaptations to environment in which the species survives. Selection favoured larger beaks, allowing for a greater variety of foods, and a wider availability of foraging opportunities. How these variations related to the habitat use by *P. caeruleus* was not studied, however there was some suggestion that the absence of *P. ater* (Coal Tit) on some of the islands had released *P. caeruleus*, and allowed it to utilize environments that it was excluded from on the mainland.

Sorensen (1997) hypothesised that the absence of a stronger, more aggressive competitor species on an island would allow a competitively inferior species to utilise a wider variety of foraging niches

The most well known morphological diversity is in the Darwinian Finches (*Geospiza sp.*) across the Galapagos and Cocos Islands (Burns *et al.* 2002). The thirteen species each show variation in bill morphology, corresponding with dietary preference (Burns *et al.* 2002). These birds are the classic example of how variations in environmental aspects influence the morphology of island species.

Like other islands, variation in morphological characteristics between mainland Australia and offshore islands does occur. This is not seen in all species, but in some instances the differences are extreme. For example, the White-winged fairy wren (*Malurus leucopterus*) shows extreme plumage variation. The populations found on Dirk Hartog and Barrow islands off the coast of Western Australia show black plumage in adult males, compared to the bright blue mature plumage encountered in mainland adults (Driskell *et al.* 2002). Genetic analysis of this trait does not show differentiation any greater

than in other populations of passerine species and the reasons behind the plumage morphology is not known (Driskell *et al.* 2002).

Abbott (1974b) examined the geographical variations in morphological traits (bill length, bill depth, bill width, tarsus length, hallux length and wing length), in 19 species of Australian bird. Four island group(s) were considered in these analyses; Lord Howe Island off the north eastern coast, Kangaroo island off the South Australian coast, Shark Bay islands (made up of Dirk Hartog and Bernier islands) off the western Australian coast and the Bass Strait Islands, including Deal Island, King Island and Flinders Island (These islands lie between the mainland of Australia and Tasmania). In the majority of instances where populations were considered, distinct morphological differences were seen between island and corresponding mainland populations.

Keast (1968a; 1970) has extensively considered the morphological variations in Tasmania's avifauna, with findings supporting those of Grant (1965) - that longer bills and legs in island birds may be linked with increased ecological versatility. These morphological trends are consistent over a variety of avian families, and in many cases habitat use and foraging behaviour are also altered, hypothesised to be because of ecological release. For example *Acanthiza pusilla* in Tasmania has a longer bill (almost 25% increased) and hallux (8% increased) compared to illustrations of this species found on mainland Australia (Keast 1970). This species also shows an increase in foliage utility in Tasmania, (approximately 25%), possibly due to the absence in Tasmania of true canopy feeders that are found on the Australian mainland (Keast 1970).

1.6 Breeding Biology

The occurrence of divergence in life history characteristics in bird species between islands and nearby mainland areas is a recognized feature in the literature (Blondel *et al.* 1992; Wiggins *et al.* 1998). Island populations tend to have lower clutch sizes (Cody 1966), later laying dates, prolonged nestling development and (in some cases) increased adult survival (Wiggins *et al.* 1998). Other characteristics such as fecundity and nesting success have also

been considered, and again in some instances, significant variation has been observed between insular and mainland populations (Blondel *et al.* 1992). Unfortunately, there is not a large literature base on this aspect of insular avifauna.

1.6.1 Clutch and egg size.

In 1954, Lack proposed a theory explaining clutch size – that birds lay the number of eggs that will give them the largest number of independent offspring (Ford 1989). From this simple suggestion, a fairly extensive body of literature has developed, in an attempt to quantify this, and other theories. Whilst consensus is still to be reached on all the factors that influence a species' maximum clutch size, there is acceptance of Ashmole's (1963) hypotheses (Ricklefs 1980). This states that reproductive rate should depend on both resource availability and the population density during the breeding season (Ricklefs 1980). Furthermore, if population size is limited by resource scarcity during non-breeding periods, then highly seasonal environments will have more resources per capita for breeding. As a consequence, clutch sizes should increase in environments where the seasonality of resource abundance is greatest (Dunn *et al.* 2000). Thus habitat stability should lead to a reduction in clutch size, and thus should be demonstrated by island avifauna.

Cody (1966) developed a theory of clutch size, the predictions with regards to island avifauna were as follows:

- As oceanic islands have climatic stability, they should show reduction in clutch size compared to mainland
- Due to reductions in predation rates, although temperate islands should have a reduced clutch size, tropical islands will only slightly differ, if at all.

Both these predictions are verified by data presented on various average clutch sizes from different regions.

Crowell and Rothstein (1981), studied Bermudan and North American passerines where, for three of the four species studied, they found significant

reductions in clutch size in the islands compared to the mainland. Interestingly, one of the species that showed this reduction was a species (*Cardinalis cardinalis*) introduced to Bermuda from the North American mainland.

Conversely to clutch size, the actual size and weight of the eggs is significantly increased in some insular populations (Higuchi 1976; Wiggins *et al.* 1998). In some instances, this is believed to be related to an increased body size in the island populations (Higuchi 1976). However, in other instances (Blondel 1985; Wiggins *et al.* 1998), the island populations are significantly smaller in size, but still show an increase in egg size. The suggestion is that reduced clutch sizes allows for greater investment in egg size and egg quality. Crowell and Rothstein (1981) suggest that as with clutch size, the variation in egg size is related to food resource availability and not a reflection of egg quality.

1.6.2 Timing of breeding and prolonged nestling development

The literature to date on this aspect of avian ecology is limited. There is evidence to suggest that divergence in the timing of breeding (Blondel 1985; Blondel *et al.* 1990) and in the period of nestling development (Higuchi 1976) occurs between mainland and island populations.

Again, studies on the *Parus* genus have been undertaken on these characteristics. Blondel's (1985) data for both *P. caeruleus* and *P. ater* suggest that both species delay breeding on the island by up to three weeks compared to mainland birds. There is evidence that also allows Blondel to conclude that nestling development may indeed be slower within the island population; however, this conclusion is based on inferences from other results and not an actual study of this characteristic. Wiggins *et al.* (1998) also encountered a delay in the onset of laying in the populations of *P. major*. The only study to conclusively show an increase in the nestling periods in island populations is that of Higuchi (1976). This increase was found to be only slight (18.3 days on mainland *cf* 19.0 days on island) but significant ($P < 0.05$). To further study the implications of parental care, Higuchi and Momose

(1981) examined the occurrence of deferred independence in young Varied Tits *P. varius*. Though sample sizes are small, the evidence implies the display of juvenile behaviours (such as begging posture and calls) can be extended up to three times longer in island populations. Higuchi and Momose (1981) conclude that the exaggerated begging behaviour and its long maintenance in island fledglings is strongly associated with the extension of the parental responsibility.

1.6.3 Success rates and longevity

Breeding success has been suggested to increase within insular environments (Cody 1966; Crowell & Rothstein 1981). The evidence to date suggests that there is no difference between successful fledging in island and mainland populations. Both Higuchi (1976) and Blondel *et al.* (1992) tested this assumption, with no significant results obtained. Similarly, there is no data to suggest that adults on islands have a greater survival rate than their mainland counterparts (Blondel *et al.* 1992), though longevity is a trait commonly associated with island avifauna (Wiggins *et al.* 1998).

These aspects of island ecology have not been considered for the Australian situation. What is interesting are the similarities in the breeding of some Australian avifauna with those seen in island populations’.

Woinarski (1985a) in his review of the breeding of small insectivorous Australian passerines compared with Northern Hemisphere species suggests that Australian passerines have a significantly reduced clutch size compared to ecologically similar species in America or Europe. Australian species also appear to have an increased incubation and fledgling period. These characteristics are more common in “old endemics”, those species that have had a longer history on the continent. Species that are relatively recent immigrants to the continent show traits more similar to Northern Hemisphere, continental species (Yom-Tov 1987).

Increased parental care has also been associated with the Australian avifauna. Russell (2000) suggests this is the “secret to the success” of the Australian avifauna. Many of the factors associated with insular or island avifaunas are

consistent with trends seen in the life history of Australia's avifauna. As with those characteristics of northern hemisphere island avifauna, the Australian attributes are ascribed to more stability in the climatic condition encountered (Russell 2000), and a decreased, though less varied, food resource availability (Woinarski 1985a).

There is no denying the evidence for the divergence of morphological and ecological characteristics in Tasmania's avifauna when compared to that of mainland Australia. However, as the Australian continent demonstrates those same characteristics (low seasonality and relative stability in resources) attributed to islands in the Northern Hemisphere, may remove these evolutionary pressures from an otherwise insular biota. It is believed that in this instance, an insular environment will not cause divergence in reproductive traits, but the physical history of the Tasmanian land mass is of greater importance and that traits demonstrated are adaptive to these conditions. Latitudinal effects may also be relevant as Tasmania is to the south of the mainland of Australia. It is also considered that the study species can in fact be considered a "continental" species, rather than an island species, with evidence to suggest that the history of this species presence in Tasmania is longer than assumed, with it being present before the Bass Strait closed (18-12,000 years ago), thus not "invading" an island environment per se, but adapting to conditions of a continental area.

1.7 Study Species

Melithreptus affinis is a small endemic Tasmanian honeyeater species (family Meliphagidae). This genus is comprised of six separate species, very similar in morphological characteristics and ecology, and believed to represent a case of recently completed speciation (Keast 1968a). The genus has been divided into three groups, based on the variation in morphology. *M. affinis* is grouped with *M. lunatus* and *M. abogularis* based on similarities in body size and plumage. However, *M. affinis* shows a reduction in bill size, bill/wing ratio and hallux length, whilst averaging a longer tarsus and tarsus/wing ratio than its allopatric mainland counterpart *M. lunatus* (Keast 1968a).

1.8 Aims

The major aims of this study are to:

- Observe and record the reproductive behaviour of a previously unstudied species of endemic Tasmanian bird;
- To construct a time budget of this species and explore the way in which it has adapted to and utilises its environment, and determine if this shows variability from a closely related mainland species.
- To explore and analyse the vocalizations of the study species
- To determine how these characteristics of an island population fit with the theories of insular adaptations.

It is predicted that the *M. affinis* will show divergence in foraging behaviour compared to mainland species, concurrent with the morphological variations already described by Keast (1968a). Reproductive traits are predicted to parallel those of mainland counterparts, reflecting the island nature of continental Australia and supporting the idea that Tasmania was colonised by the study species whilst the Bass Strait land bridge was exposed.

The thesis is structured in three sections. Section one (chapters one and two) provides background information on the Tasmanian environment, site descriptions and methodology.

Chapter two provides a description of study sites and an in-depth account of the field methodology utilised throughout the study. This chapter includes a revision of time budget methods and highlights the need to define what a study is to achieve with regards to methodology employed to construct timebudgets. Statistical analysis is treated separately in each of the results chapters.

Section two (chapters three through eight) provides the results of field studies on *M. affinis* and covers basic life history, feeding ecology, habitat use and breeding ecology. It also includes a study on the vocal characteristics of the species across its southern range.

Chapter three provides the basic ecology of *M. affinis*. This chapter also provides an analysis of banding data obtained from the Australian bird and bat banding scheme. It attempts to answer some basic questions on the life history, movements and flocking of the species.

Chapter four explores the time budget of *M. affinis*. This considers behaviours, feeding method, seasonal and diurnal variations. This chapter highlights the flexibility of the species during drought conditions and its ability to utilise a variety of resources depending on environmental conditions. This chapter is presented in the form of a scientific paper.

Chapter five explores the microhabitat use and tree species utilized by *M. affinis*. Again, the implications of drought conditions are considered.

Chapter six provides the results of the only study on the breeding biology of this species. The content of this chapter raises questions as to the validity of island biogeographic theory with regards to breeding biology in Tasmanian avifauna. The results suggest a history for *M. affinis* dependant on the geological history of the landmass.

Chapter seven examines the behaviours of *M. affinis* during the nesting cycle. It considers the occurrence of courtship feeding, and the provisioning of incubating females by accompanying birds. The provisioning rates of nestlings and fledgling are explored, as is the impact of drought conditions and the presence on non-breeding adults on provisioning rates.

Chapter eight provides an analysis of the vocal repertoire of the study species. Calls were collected across the south-east of the state, and also includes sample calls from Maria and Bruny islands.

The final chapter (nine) provides a general discussion on the results obtained placing them in the context of current biological theory. It shows that although this endemic avian species conforms to aspects of biogeographic theory, it does not conform to them all, further highlighting the difference in species ecology between Australia and the Northern Hemisphere.

This chapter also highlight areas of further research and the limitations of the current study.

2. GENERAL METHODOLOGY

2.1 Introduction

The purpose of this study was to determine basic life history characteristics for a previously unstudied endemic island species. This included exploration of population dynamics, general behaviour and habitat usage, breeding biology and the vocalization of the study species.

To do this, studies were undertaken between August 2000 and April 2003, encompassing three breeding periods of the study species *Melithreptus affinis*, a small endemic honeyeater species.

This field study was combined with the collation of historical documentation, records and specimens from a number of museums and scientific institutes, to begin to understand the ecology of this species.

2.2 Study Landscape.

Six main field sites were used around the greater Hobart area (42°48', 147° 26' Figure 2.1), on both the eastern and western sides on the Derwent River. Sites were selected for two main reasons. These were:

- 1 *M. affinis* was consistently encountered at the site all year round,
2. The vegetation types were consistent across all sites.

2.2.1 Topography

The Derwent River dominates the topography of the landscape around Hobart. The prevailing landscape is of hills and associated flats (Davies 1988), being dominated by Mount Wellington on the western shore and the Meehan Ranges running the length of the lower Derwent on the eastern shore. Plains are not extensively developed in the study area but tend to be associated with the river system (Davies 1988).

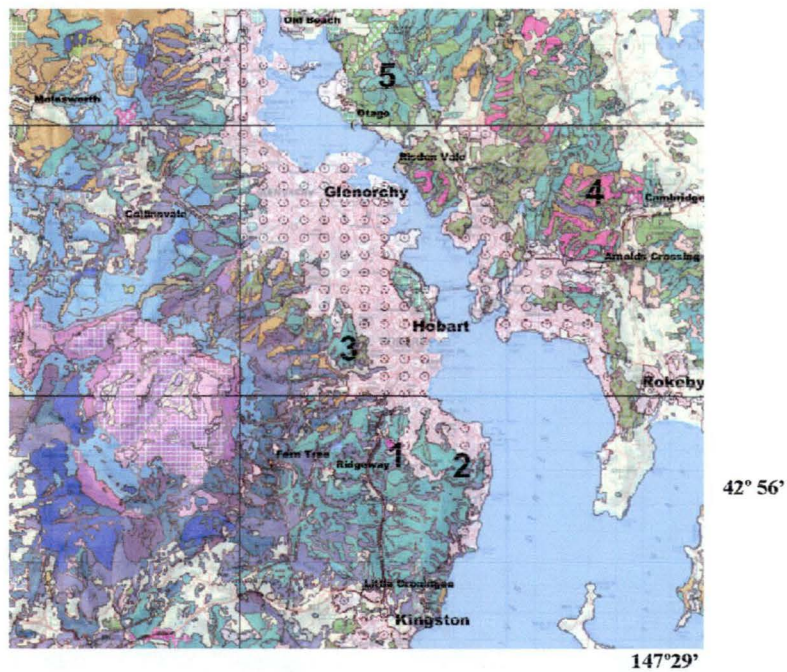


Figure 2.1. Location of field sites used during study. 1 Ridgeway Reserve, 2 University Reserve, 3 Knocklofty, 4 Meehan Ranges, 5 Mount Direction. Area in white with black circles represents current inhabited areas, cream areas represent land clearance. Remaining coloured areas represent remnant vegetation as per the current TASVEG GIS layer.

2.2.2 Geology and soils

All sites, on both the eastern and western shores of the Derwent River, have a geological base of Jurassic Dolerite (Davies 1988). Dolerite bodies cover vast areas of the south and east of Tasmania. Intrusion of dolerite occurred approximately 165 million years ago with the break up of Gondwana (Davies 1988).

The soil type on the exposed and upper slopes of the study region is classified as loam, progressing through a clay loam on the slopes to a medium clay soil type on the drainage flats (Davies 1988).

2.2.3 Climate

The Tasmanian climate is classified as a temperate maritime climate, because the state is an island and at no point more than 115km from the sea (Davies 1988).

Coastal temperatures tend to display a smaller range than inland temperatures, with a mean maximum of about 18°C to mean minimum of about 9°C. Table 2.1 presents this data for three weather stations located in proximity to current study sites. The temperatures obtained from Mount Wellington are those records from the summit of the mountain, and it must be noted that these are at the extreme end of the regional range, with temperatures across field sites falling below this range.

The sites in the study area fall into three rainfall bands as defined by Davies (1988). These are the 500-600mm, 600-700mm band and 700-800mm band. The lowest rainfall band is across the more eastern sites, increasing towards Mount Wellington. Rainfall across Tasmania tends to be evenly distributed across the year (Davies 1988), and though this trend continues in the study region, there are discernable variations in the monthly rainfall. Generally, January, February and March show the lowest monthly rainfall when weak high-pressure systems control the weather patterns, with highest rainfall occurring from August through October (Davies 1988).

During the study period, rainfall across the study region was considerably reduced. Figure 2.2 shows the average monthly rainfall from 1997-2003 for

each of the three sites. Both late 2000 and 2002 show a lower rainfall rate than other years. There is also a switch from patterns defined by Davies (1988) with much of the rainfall occurring across the summer months.

Table 2.1 Climatic characteristics of the study area. Values obtained from the Bureau of Meteorology (2004).

| | Mount Wellington¹ | Cambridge² | Hobart³ |
|-----------------------------------|-------------------------------------|------------------------------|---------------------------|
| Mean daily max. temp. °C (annual) | 7.5 | 17.4 | 16.8 |
| Mean daily min. temp. °C (annual) | 1.2 | 8 | 8.3 |
| Mean annual rainfall (mm) | 907.1 | 502.6 | 619.3 |

¹ Mount Wellington summit weather station

² Hobart airport, Cambridge weather station

³ Hobart, Ellerslie Road weather station

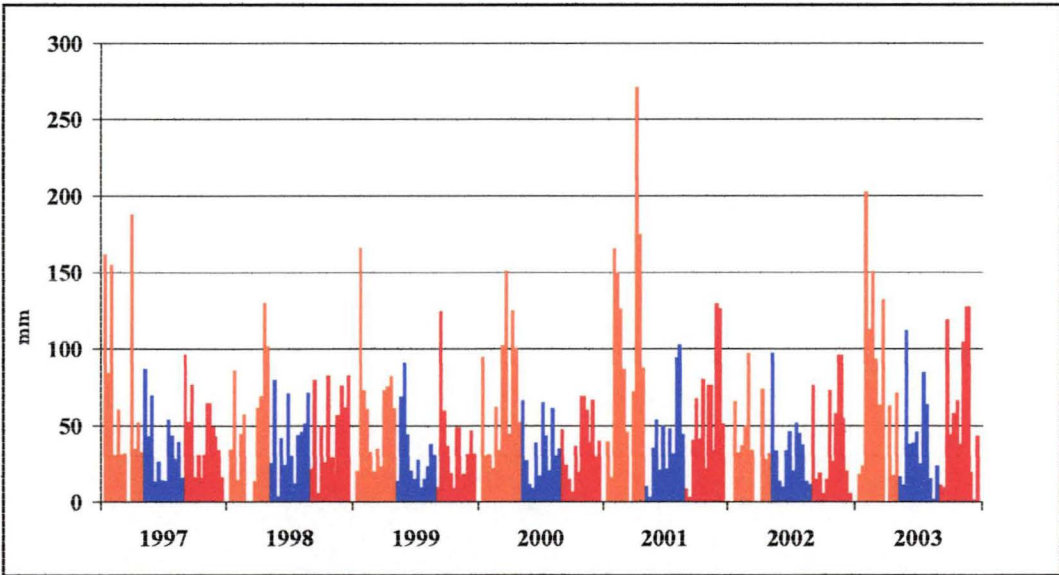


Figure 2.2 Average monthly rainfall for the Mount Wellington summit weather station (orange) Hobart airport, Cambridge weather station (blue) and Hobart, Ellerslie Road weather station (red) representative of the field sites used in this study. Of note are the low rates of rainfall in late 2000 and across 2002. Data obtained from the Bureau of Meteorology (2004).

2.2.4 Vegetation

The major vegetation types across the field sites used in this study have been defined by North (1997; 2000) as DRY–gPULC *Eucalyptus pulchella* grassy woodland, DRY-shPULC – *E. pulchella* shrubby forest and DRY –shOB – Shrubby *E. obliqua* dry sclerophyll forest.

DRY–gPULC *Eucalyptus pulchella* grassy woodland is a community occupying well-drained slopes on dolerite. *Eucalyptus viminalis* and *E. globulus* are often co-dominant with *E. pulchella*. Understorey vegetation tends to be a scattered shrub layer of *Busaria spinosa*, *Dodonaea viscosa*, *Acacia dealbata*, *A. mearnsii* and *Exocarpus cupressoides*. Grasses are dominated by *Poa rodwayi* and *Themeda triandra* (North 1997; 2000).

DRY-shPULC – *E. pulchella* shrubby forest supports a similar array of plant species to the above described vegetation type. Other *Eucalypt sp.* are not co-dominant however (North 1997; 2000).

DRY –shOB – Shrubby *E. obliqua* dry sclerophyll forest. This vegetation type is interspersed throughout the above described vegetation types, occupying areas of higher moisture content. It is typical of areas that would support wet forests if a reduction in the incidence of fire regime occurred. Prominent understorey plants include *Bedfordia salicina*, *A. verticulata*, *A. melanoxylon*, *Pultenaea daphnoides* and *Goodenia ovata* (North, 1997; 2000).

Across each of the sites used in this study the dominant vegetation assemblage fits into one of the above categories.

2.3 Site Description

2.3.1 Ridgeway Reserve (plates 2.1 and 2.2)

Ridgeway Reserve is located approximately 3km from the central business district of Hobart. The reserve is managed by Hobart City Council, and is a major water catchment site for the Browns River (Elton 1997). The two main sources of Hobart's water supply – Ridgeway Reservoir and the Waterworks Reservoirs are also located within the Reserve. The reserve covers an area of approximately 500 hectares (Elton 1997) typical land use is for water catchment, grazing and recreation (Davies 1988).

For the purposes of this study, Ridgeway Reserve was partitioned into two distinct sites, located approximately one kilometre from the each other. Site RW (42° 55' 30'', 147° 17') was located at the higher altitude (400 – 500m asl). This area is in close proximity to the townships of Ridgeway and Ferntree and shows varying degrees of disturbance. Areas have been cleared for recreational use, as well as large corridors cleared under power lines. Areas have an understorey dominated by the introduced Gorse (*Ulex europaeus*) and as such are exposed to ongoing weed management, in the form of constant bulldozing of the weed infestation.

Site RR (42° 55', 147° 17' 30'') is located within the reserve, but closer to Hobart, with a lower elevation (300 - 350m asl). This site includes the vegetation proximal to the Ridgeway Reservoir, which was built in the 1880's. This area of vegetation was most recently subjected to fire in 1998 and as such supports a different structural habitat to that of site RW.

2.3.2 University Reserve

This reserve is situated on Mount Nelson (42° 55', 147° 19'; 200-220m asl) and encompasses approximately 83 ha. The University of Tasmania manages the site, with the northern section allocated to sports fields. The rest of the reserve is used for teaching and recreational purposes. The site was most recently subjected to fire in 1995.



Plate 2.1 Ridgeway Reserve site RW



Plate 2.2 Ridgeway Reserve site RR

2.3.3 Knocklofty Reserve

Knocklofty Reserve is a bushland park 122ha in size (Knocklofty Reserve Fire management plan 1998). It is comprised of the slopes and the summit of Knocklofty, a prominent hill on the outskirts of Hobart (42° 53', 147° 18'; altitude 100m – 374m asl). Adjoining land uses to the reserve include residential areas and an abandoned quarry to the north, residential areas to the east, and bushland (privately owned and council land), landfill sites and bushland reserves to the south and west. These tracts of bushland connect the reserve to Wellington Park (Knocklofty Reserve Fire Management Plan 1998).

The area supports vegetation comprising of wet forest along the lower south-facing slopes, dry grassy woodlands and grasslands. It was last most recently burnt in 1993.

These sites are all located on the western side of the Derwent River. They are all relatively large, minimally disturbed areas, interlinked with Wellington Park, an 18 250ha reserve encompassing Mount Wellington and surrounding bushland

2.3.4 Meehan Ranges Recreational Reserve (plate 2.3)

The Meehan Ranges is a geological feature that runs approximately 30km along the eastern side of the Derwent River. It extends from Brighton in the north (42° 42', 147° 16') as far south as Rokeby (42°54', 147° 28'). Field studies have taken place towards the south end of the ranges near Cambridge, 15km east of Hobart (42° 50' 30'', 147° 24'). The area utilised for field studies has been declared a nature reserve. However, this reservation status tends to be overlooked, and the area is highly impacted upon by both motorcycles and bicycles along the creek line. Approximately a 1km x 1km section of the range was used during this study.

The vegetation of the study site varies as Barilla Rivulet; a permanent creek runs through the centre of the study area. Canopy vegetation along the creek consists generally of *E. globulus*, *E. obliqua* and *E. rubida*. Further back as the slope steepens the canopy is dominated by *E. viminalis* with sporadic *E.*

pulchella. Patches of the locally endemic *E. risdonii* also occur throughout this area, along with stand of *Allocasuarina* sp. Understorey is dominated by *Exocarpus cupressiformis* and *A. dealbata*.

2.3.5 Mount Direction (plate 2.4)

This is a tract of land managed by Clarence City council. It is located approximately 15km to the north of Hobart, on the eastern shore of the Derwent River (42° 49', 147° 25'). Only the western slopes of the mountain were surveyed during this study. The eastern side of the mountain is a part of the Risdon Brook Reservoir catchment, the major water supply of Clarence City.

The vegetation of this site is relatively undisturbed, dominated by *E. pulchella* and *E. viminalis*. As with other site selected, *E. globulus* is also present though as a sub-dominant species. The understorey is open grassy woodland, with *Acacia* sp. and *Bursaria spinosa*. Stands of *Casuarina littoralis* are prominent on some of the more exposed slopes.

The land is reserved for conservation and utilized for low impact recreational purposes.



Plate 2.3 Meehan Ranges



Plate 2.4 Mount Direction

2.4 Field Work and Data Collection

From August 2000 through to the end of February 2003 the above sites were regularly visited to obtain field data and observations of *M. affinis*. During the breeding period (September to early February), field sites were visited at a minimum once a week in the search for nesting attempts. During this time, observations were also taken for time budget construction. Where nest attempts were located, these were monitored every one to two days.

During the non-breeding period, field trips were subject to weather conditions, with visits being undertaken whenever conditions were suitable.

2.4.1 Life History

The data used for this section of study (chapter 3) were that of historical records obtained from the Australian Bird and Bat Band Scheme, co-ordinated by Environment Australia. Data obtained from this scheme were the banding records covering a period from 1965 – 1992. The banders responsible for the collection of this data are listed in appendix 1.

All records contained information on location of banding, date and whether birds were new or recaptures. Some records provided an age estimate of individuals, others simply if birds were juveniles or adults. There was also some morphological data provided, generally weight, wing length and tail length. Total head length, bill length and tarsus length were provided for some records.

Where possible, this data was analysed using the Jolly-Seber method (Seber 1986) to estimate population sizes. Also this data was analysed to obtain an indication of annual breeding patterns. The proportion of juvenile birds in each year group of banding records was calculated, providing a gross indication of juvenile birds within the population and of breeding cycles in this species.

Flock sizes were recorded in the field whenever birds were located.

2.4.2 Mist Netting and Colour Banding

Individual birds were to be colour banded using standard celluloid colour bands of size two. Darvic material was used for yellow bands, as celluloid bands were not available in this colour. Metal number bands were also given to individual birds. Band size for Black-headed Honeyeater (sp no. 584) is 2 as determined by Australian Birds and Bat Banding Scheme (1st ed 1989 – manual compiled by K. W. Lowe).

Mist-netting using a 25mm meshing will be applied to catch and individually colour band birds using a combination of three colour rings plus metal band. This is to allow for individual birds to be recognised at nest sites. Exploration for appropriate net sites began 7th August 2001, with first netting attempt 22nd August 2001. Up to five nets a session were employed.

Birds were targeted using both call back and decoy birds.

Territorial calls of *M. affinis* were recorded at the Ridgeway site and used in an attempt to lure birds into nets during the breeding period. These calls were combined with a paper machè bird, as previous netting experience found that if one bird is entangled, then generally the rest of the flock would respond to the vocalization of this individual (A. Fletcher pers. com.).

Calls of other birds, along with decoy birds were also tried. The calls of Pallid cuckoos (*Cuculus pallidus*) and Shining Bronze-cuckoos (*Chrysococcyx lucidus*) were played, and again, *M. affinis* showed some response to the calls.

Once netted, measurements of the following morphologies were recorded:

- Age
- Weight
- Tarsus length
- Total head length
- Tail length
- Wing length

These morphological attributes were then used to assign gender to birds

based on the measurements of Henderson and Green (1982).

Methods on sexing individuals were explored, particularly for a non-invasive method. HANZAB (2001) show similar morphological variation between the sexes as of Henderson and Green (1982), with males being significantly larger than females. This allowed sexing on site in the field when a breeding pair was identified. The adult male bird is obviously larger than the female. Data from museum skins from Australian Natural Wildlife Collection, CSIRO shows that only the female develops a brood patch during the breeding period, which in some instances can be distinguished through binoculars.

A third method was tested to allow non-invasive sexing. This involved the use of Ultra Violet light. In some avian groups, particularly Psittaciformes, the sexes fluorescence under UV light (Hausmann *et al.* 2003). This fluorescing is generally found in the plumage of the birds. Though no bio-fluorescence has been noted in the Meliphagidae plumage, it was thought that perhaps the skin above the eye in *M. affinis* might show sexual differences. Museum skins held at the Tasmanian Museum and Art Gallery were exposed to both UV near (freq) and UV far (freq) light, with neither showing any luminescence in the species.

2.4.3 Time Budget

Data was collected opportunistically from September 2000 to August 2002. This encompassed two breeding and two non-breeding seasons.

Only adult birds were sampled. Birds were located by either sight or call. Once an individual was located for observation it was observed until a change in behaviour occurred from that originally encountered. This was done to reduce the risk of biasing data towards obvious behaviours. Once located, focal individuals were followed for as long as possible.

Observations during the breeding season were not taken directly around nests (though interactions at nests were recorded if they subsequently occurred during the observation period), as it was general behaviours, not specific breeding behaviours that were of interest in this particular study. Both

breeding and non-breeding birds were potentially sampled, as individual birds were not distinguishable.

Individuals were watched for as long as possible, ending if a bird was lost from the observer's view.

Observations consisted of the focal individual being followed with behaviours being vocally recorded onto a hand held SONY® V.O.R microcassette – recorder M-530V, into which the observer recorded a continuous description of the behaviour.

Behaviour was allocated to one of nine categories:

- Glean (GL): When bird was seen to be searching out and feeding within the foliage, on the foliage.
- Probe (PB): This category included all observations of individuals when feeding on trunk or branches of a tree. This included probing under bark as a method of obtaining food as well as feeding directly off the trunk of the tree. It is possible that feeding on manna was occurring.
- Fly (FL): When individual was in the air. This included when birds moved between Branches whilst feeding. This was recorded as both the time spent flying plus an estimate of the distance flown.
- Perch (PE). This behaviour was allocated when an individual was stationary
- Preen (PR): This behaviour was allocated when individual was observed to demonstrate any type of grooming.
- Interspecific/Intraspecific Interaction (IA): Any interaction with another birds was recorded, including the species of bird and whether or not the focal species was the aggressor or on the receiving end of an attack.
- Move (MV): This behaviour was allocated to an individual when it was moving throughout the vegetation but not actively feeding.

- Nectar: this category encompassed all observations of individuals feeding within blossoms.
- Hawk: This behaviour was recorded when an individual was observed taking prey on the wing.

Total foraging time was calculated by combining glean, probe and nectar. Hawking behaviour was not included in foraging as the frequency of this behaviour was low and as it tended to be a one off behaviour, it was difficult to calculate the duration of the behaviour. These behavioural groups are consistent with groups allocated in other studies (Collins & Briffa 1983; Recher & Gebski 1990).

The tree species in which the individual was observed was also recorded as was a 'microhabitat' variable. This was one of five different habitats:

- Upper Canopy: defined as the upper third of a tree
- Mid Canopy: defined as the mid third of a tree
- Lower Canopy: defined as the bottom third of the tree
- Understorey: any noted observations within the shrubby lower layers of vegetation
- Ground: this is self-explanatory.

Records were then transcribed from recorded vocal observations. This was done in two ways, reflecting the main methods applied in the literature (Collins & Briffa 1983; Recher & Gebski 1990; Kersten 1996; Oliver 2001.)

Firstly, behaviour was timed with a Sportline® Watertight stopwatch to the nearest 0.1 second. Total time (or REAL time) of each behavioural group was collated from these records (Oliver 1998).

Secondly, a record was taken of the focal birds behaviour every ten seconds (Altman 1974 continuous instantaneous sampling techniques) and thirty seconds, calculating a frequency of occurrence of behaviours.

The two methods were applied as they provide different information about the behavioural habits of the focal species. The first method allows a complete breakdown of the proportion of time spent undertaking each

different behavioural category. This is, however, at the expense of any order to the behaviour and so patterns tend to be lost. The second method allows the order of behaviours to be observed but measures the frequency of behaviours rather than the actual amount of time allocated to each behavioural group. At each ten-second interval the behaviour is recorded for what the focus is doing at that exact point in time. If multiple behaviours occur within the sample time these are not recorded, resulting in an underestimate of some behaviours. Conversely, the same can happen if a behaviour consistently falls at the ten second mark, it can be perceived as being proportionally more frequent than another behavioural category which, in reality accounts for a greater time proportion of activities.

These two methods were compared statistically to determine if significant variation occurred in the proportional estimates of behaviours. If there was variation, it becomes important for researchers to determine what it is they are want to measure, and then which method best allows for these measurements to be taken (Appendix 2 provides the statistical comparisons of the method types).

For this study, it was decided to use realtime records because it was the changes in time allocated to behaviours between breeding and non-breeding that was of interest and using realtime measurements were felt to give a more accurate representation of commitment to each behaviour by the study species.

Two breeding and two non-breeding seasons were sampled for time budget observations. Breeding season consisted of September through to February where behaviours such as bonding and courtship feeding through to the feeding of offspring were apparent in the study species. The non-breeding season was the remaining six months. The four seasons were as follows: 2000- 2001 breeding season, 2001 non-breeding season, 2001-2002 breeding season, 2002 non breeding season.

Time budgets were compared across breeding and non-breeding periods as well as a comparison made across the four different sample period.

Diurnal comparisons were also made across the data set. Diurnal periods

were calculated based on the azimuth, or angle of the sun along the horizon. This method was applied, as there was concern that comparisons would not be accurate between seasons if an arbitrary division of the data set based on time periods was applied. This is to take into account the variation in the duration of day length in Hobart between mid summer and mid winter. Daylight hours in Hobart can vary from 16 hours of light mid-summer to 10 hours in mid-winter. Sunshine hours can vary from 8.5 in January to 3.0 in June (Davies 1988). Subsequently, comparing avian activity at 3pm in the height of summer will differ to that mid winter when day length and sunlight hours differ substantially. A method to standardize time periods was employed for this reason.

Azimuth were calculated using an online calculator program provided by the Astronomical Applications Department of the U.S Naval Observatory, located at:

<http://aa.usno.navy.mil>

This site involved entering the location and date of desired angle measurements plus a correction value based on time differences between Greenwich time and local time. The program then produced the necessary measurements.

2.4.4 Breeding biology

A combination of field based research and the collation of museum records was employed to determine aspects of the breeding biology of *M. affinis*.

Museum records

Five institutions were contacted to determine the availability of historical records of *M. affinis*. These were the Australian Museum Sydney, the Museum of Victoria Melbourne, Queen Victoria Museum and Art Gallery (QVMAG) Launceston, Tasmanian Museum and Art Gallery (TMAG) Hobart and the Australian Natural Wildlife Collection (ANWC) located at C.S.I.R.O. Sustainable Ecosystems in Canberra. Each of these institutions had some records, ranging from skin data to nest or egg collects.

Twenty-nine nests held at QVMAG were described and measured. Measurements were taken using scientific callipers of the internal and external diameter of the nest cup, the length from nest lip to the base, the internal depth of the nest cup. Nests with no leaf or twig matter present in sample were weighed using spring scales. Descriptions and diagrams were made of the building material and the design of the nest suspension. Data of tree species, nest height and date of collection were also taken from these samples, as well as records of clutch size if included.

Ian Mason at ANWC provided egg measurements. Fifty-four individual eggs, comprising 18 clutches were measured, taking a measurement of length and breadth. From these measurements the circumference of the eggs were calculated. Along with these measurements, copies of the original logbook were provided, giving the location where clutches were collected, the date, the tree species, nest height and any other observation taken at the time of collection. Robert Palmer, also at ANWC, provided copies of all skin data held by the collection. This included reproductive traits such as gonad size/development and brood patch.

Data from the three capital city museums consisted only of skin data and has not been incorporated in this study.

Field data

Nest observations were undertaken wherever a nest was found, regardless of when in the breeding cycle it was. Some nests were observed from building, whilst other observations began at incubation, nestling and in some instances after young were fledged.

Nests were located by observing the behaviour of adult birds. If an adult was observed displaying a behaviour that could be assumed to be breeding related (such as spending extended periods on the ground) or collecting plant materials, they were followed until nest site was located.

The following characteristics were recorded when nest sites were found:

- Site
- Date

- Nest ID (was allocated a code based on the site and the order of location and year ie: second nest found at Ridgeway in 2001 was RW201)
- Tree Species – this is limited by the vegetation at sites
- Height of nest and nest tree – this was calculated by measuring the distance to the trunk from a fixed point, and then from this same point measuring the distance to the nest with a Leica LRF 800 range master. The distance from the centre trunk the nest was suspended was subtracted from the basal length measured. Using an assumption of 90° angle between tree trunk and line of sight, Pythagoras' theorem was applied to calculate the height of the nest. To this was then added a measurement of the eye height of the observer, as measurements to the trunk were made at eye line height. Care was taken to maintain the same contour when taking measurements. Tree height was measured using the same method.
- Distance nest is suspended from central trunk
- Percent of foliage cover around nest – this is an arbitrary scale based on the observers judgement of cover
- Tree circumference at the observers' chest height was measured to provide an arbitrary indication of tree age selected for.
- Distance to closest nest – active or past nest.

These nest observations were used to determine incubation period, nestling period and fledging behaviours. This data was also used to calculate nest success. Mayfield's (1975) method was employed.

2.4.5 Parental Investment

To determine the investment made by *M. affinis* to juveniles over all stages of breeding, detailed observations were taken at each reproductive attempt located.

Four nesting stages were allocated. These were:

1. Building – where nest construction was undertaken

2. Incubation – period of time where adult birds were observed sitting on eggs
3. Nestling – period of time from hatching of eggs to juveniles leaving nest (beginning judged by parental activity of the feeding of young)
4. Fledgling – period after young have left nest.

Observations of building behaviours were taken for as long as possible, due to the reduced chance of finding nests at this stage, and thus as much information was collected when ever possible. Observations ceased when building activity decreased.

For other nest stages, nests were monitored second day at a minimum. This was to limit the interference at nests (though birds appeared to show no response to observer presence) and any greater time difference between observations would make determining events difficult.

Observations of activities at the nest were taken over an hour long interval. This time period was chosen as it was the maximum period the observer could retain a high level of concentration and focus on the nest under observation, and thus reduce the chance of observer error. These hour intervals were taken across three diurnal periods to determine if these temporal characteristic influences the effort invested by adults in the raising of juveniles. These periods were defined as morning (sunrise – 10:30am), midday (10:30am- 2:30pm) and afternoon (2:30pm – sunset).

These sampling classes (of an hour within a temporal group) were applied to incubation and nestling phases. Subsequently, sampling was standardised for each observation. If for some reason, for example weather changes, observations did not last the entire 60 minute period further observations were taken to total the 60min observational period. These were tested for significant variations and pooled if found to be insignificant.

At each nest site, using a hand held SONY® V.O.R microcassette – corder M-530V vocal records were made.

For incubation observations, initial time was recorded, and allocated time zero when data was analysed. At the start of each observation, it was noted if

birds were on or off the nest. Throughout the observation period, records were taken when birds left from incubation, returned to incubate, and the occurrence of other birds (male or otherwise) visiting the female whilst incubating. These visits by other non-incubating birds were determined to be either incubation feeding or visits without feeding occurring.

Similar records were taken during the nestling period. Again, start time of recorded observation was noted, when an adult entered the nest tree, when they attended the nest, when the adult left the nest site and if this leaving was directly from the nest or via another area of the nest tree. Gender was also allocated to adult birds where possible.

Using a stopwatch, the time at which each observation was taken was recorded with the beginning of each observation being allocated time zero. The time measurements were recorded to 0.1 of a second. By determining the time of each behavioural event, relative to start time, the time interval between each behaviour was calculated, allowing for a rate of incubation, visits or behaviours to be calculated. It was this time interval measurement that was then used for statistical analysis.

For fledgling behaviours, as previously stated, these were taken incidentally, due to the mobility of juvenile birds. Thus the duration of observation period could not be controlled and observations lasted as long as possible. Again, records were made vocally onto a handheld SONY® V.O.R microcassette – recorder M-530V, and notes were taken of start time, attendance of juveniles by adult birds, the sex of the adult (when possible) and the number of juveniles fed by adults at each feeding bout. Notes were also taken on which individual young each adult fed, but as birds were not individually identifiable, these were highly speculative.

Again, using the start time as time zero, the interval between feeding bouts was calculated, resulting in a feeding rate. This interval was used in data analysis.

2.4.6 Call Analysis

Field recordings.

To determine if the calls of *M. affinis* differ with geographic location, a range of calls was recorded from unbanded birds across 9 different locations (see Chapter 8, figure 8.1 for locations). Calls were mainly recorded over the breeding period, though some calls recorded during the non-breeding period have been included in the analysis. These non-breeding calls are records of general contact calls used by the species all year round, and subsequently inclusion in analysis will not impact upon the results. Not all song types were recorded for each site.

Calls were initially recorded using a Sony TC- D5m Capstan Server Stereo Cassette recorder, with a Nikamich CM – 300 condenser microphone with CP-4 shot gun attachment. This was replaced with a Sony Portable Minidisc recorder, MZ – N707, with the same microphone, which was lighter and more compact for field work. As calls were recorded onto minidisc they were in digital format from the initial recording, reducing the loss of sound quality through the downloading process. Calls originally recorded with the cassette recorder were recorded onto minidisk for downloading.

Song analysis

Recorded calls were entered directly into the computer program Syrinx (John Burt, www.syrinxpc.com) to generate spectrograms. These were produced to allow an analysis of changes in the call frequency with time.

Three levels of classification were applied to the vocalizations recorded, and analyses were undertaken at each level. These classification levels were:

1. Call: allocated by visual classification of spectrograms (Tracy & Baker 1999) and sound of call, combined with an understanding of the behavioural traits associated with the production of the vocalization.
2. Phrase: the finite vocalizations of individuals within each call type. These ranged from single to multi-syllable songs.
3. Syllable: the individual components that an individual vocalizes that make up a song.

For each relevant syllable displayed on a spectrogram the following variables were measured in order to analyse vocalizations.

The variables measured were:

1. Beginning time of syllable
2. End time of syllable
3. Syllable length (secs)
4. Between Syllable time (secs)
5. High frequency (KHz)
6. Low frequency (KHz)
7. Band width (KHz)
8. Beginning frequency (KHz)
9. End frequency (KHz) (figure 8.2)

For calls where harmonics occurred, the strongest signal was measured, with a record taken of the number of harmonic peaks (Kentish *et al.* 2001). Any peaks or troughs encountered in syllables were also noted, with a record taken of the frequency of the peak or trough, plus the time at which the change occurred, allowing for the time interval between the beginning of the call and the peak/trough to be calculated.

2.5 Statistical Analysis

Throughout this study both parametric and non-parametric statistical techniques were employed.

Non-parametric methods used were:

- Kruskal-Wallis non-parametric Analysis of Variance (ANOVA). This test is equivalent to an one-way ANOVA, and is appropriate when the assumptions of population normality and homogeneity of variances are not met by the data (Coakes & Steed 1996)
- Mann-Whitney U test. This statistical procedure tests the hypothesis that two independent samples come from populations having the

same distribution. It is equivalent to the independent group t-test (Coakes & Steed 1996).

- Wilcoxon Signed Rank test. This is the non-parametric equivalent of a repeated measures ANOVA. This method allows the same individual to perform under different independent variables (Coakes & Steed 1996).
- Chi-squared test for independence or relatedness.

For parametric statistical procedures, both univariate and multivariate methods were employed. Parametric methods used were:

- ANOVA – one way (type I) This allows for a test statistic to be calculated using two derived estimations of population variance from the data. Population estimates are derived for within-group variation and between-group variation. This statistical method allows for the comparison more than two groups to determine if their population means are equal (Coakes & Steed 1996).
 - two-factor with unequal replications. This works on the same principle as a simple one way ANOVA, but allows for a second *independent* variable to added (Coakes & Steed 1996; Zarr 1999)
- Analysis of Covariance (ANCOVA). This method is a variation of an ANOVA. It allows for the testing of an independent variable, by statistically controlling the influence of an extraneous variable (covariate) on the dependant variable. This method reduces error variance due to individual differences (Coakes & Steed 1996)
- Multivariate Analysis of Variance (MANOVA). This statistical procedure is again an extension of ANOVA, but is used when there is more than one *dependent* variable (Pallant 2001). By analysing data using MANOVA, it reduces the chance of type one errors. Also, this procedure is more robust than simple analysis of variance and thus data does not have to fill assumptions as stringently as in univariate analysis (Pallant 2001)
- Multidimensional Scaling. This is a statistical technique that analyses the dissimilarity within a data set by making pair-wise

comparisons within a data matrix (Norusis 1994). This results in a plot where objects are positioned in a multidimensional space and the distance between objects corresponds to the dissimilarity between them (Clarke 1993)

- Principal Component Analysis (PCA). This multivariate method allows for data to be reduced in such a way that the dependant variables that contribute the greatest significant variation are isolated. PCA transforms original variables into a smaller set of linear combination, with all variance in the variables being used (Pallant 2001). Once isolated, significant variables are rotated, in this study, using orthogonal: Varimax approach, which attempts to minimize the number of variables with high loadings on each factor (Pallant 2001).

Proportional data was transformed using the Freeman & Tukey, (1950 cited in Zarr, 1999) equation:

$$p' = \frac{1}{2} [\arcsin\sqrt{X/n+1} + \arcsin\sqrt{X+1/n+1}]$$

This was used as much of the data was at extreme ends of the data range (ie near 0 or 100%) (Zarr 1999). Arcsin transformation increases the spread of proportional data, normalizing the distribution, and thus allowing for parametric statistical techniques to be applied (Zarr 1999).

Where multiple non-parametric tests were undertaken, Bonferroni adjustments were made to the normal alpha value of 0.05. That is 0.05 was divided by the number of tests undertaken. Bonferroni adjusted alpha levels are given in chapters where needed.

3. LIFE HISTORY AND ECOLOGY

3.1 Introduction

There are many aspects to specie's life history, uniquely suited to the purposes of that species. These evolve in response to the different environmental impacts on survival and fertility within different age classes (Partridge & Harvey 1988). This information is the baseline information essential if any further study is to be undertaken on an organism. It is also this data that is imperative if a species becomes threatened and it becomes necessary to implement management strategies. Subsequently, this chapter attempts to answer some of these questions.

The first section of this chapter is a review of the ecological data currently available on the study species *Melithreptus affinis*. What this shows is the limit of what is actually known on this species. The *Melithreptus* genus remains relatively unstudied, and to date only three published studies are available on *M. affinis* (Brent 1905; Thomas 1980; Slater 1994). The overall aim of this research project is add to the scientific knowledge on this species.

The second section of this chapter is given to analyses of banding data obtained from the Australian Bird and Bat Banding Scheme. The aim is to explore the life history information provided by this data.

3.2 Ecology

3.2.1 Family MELIPHAGIDAE

This family comprises 42 genera, 182 species, distributed across Australasia (Gill 1995). Sixty-seven species are found across the Australian continent (Schodde & Mason 1999). Most Meliphagids are nectarivorous to some degree, with the most striking family characteristic being that of a "brush tongue". The tongue, in its structure, is notably different from other avifauna with similar habits in that it is prolonged and protrusible; the basal part is curled up on each side, forming two long grooves; the distal section of the

tongue is divided into four sections, each of which is ‘frayed’ along the edge, combining together to form a brush (Sibley & Ahlquist 1990).

Though commonly referred to as ‘honeyeaters’, few of the members of this family are totally dependant on nectar as a food source. Other forms of carbohydrates are utilised such as manna, honeydew and lerp (Paton 1980). The dependence on carbohydrate sources vary with species. Table 3.1 provides a simple estimate of the average dietary importance played by nectar across genus with Meliphagidae.

Table 3-1 Comparison of percentage nectar use in genera of the family Meliphagidae. Values given are based on Pyke (1980).

| Genus | Percent of nectar use | Genus | Percent of nectar use |
|------------------------|-----------------------|---------------------|-----------------------|
| <i>Meliphaga</i> | 17 | <i>Anthochaera</i> | 38 |
| <i>Xanthotis</i> | 17 | <i>Acanthagenys</i> | 38 |
| <i>Lichenostomus</i> | 22 | <i>Myzomela</i> | 56 |
| <i>Manorina</i> | 28 | <i>Certhionyx</i> | 56 |
| <i>Melithreptus</i> | 31 | <i>Phylidonyris</i> | 57 |
| <i>Acanthorhynchus</i> | 39 | <i>Lichmera</i> | 60 |

3.2.2 Genus *Melithreptus*

The honeyeater genus *Melithreptus* contains six species with distributions across Australia. Five of these species are endemic to Australia, with two being confined to Tasmania only (Black-headed Honeyeater, *M. affinis*, and Strong-billed Honeyeater, *M. validirostris*). The White-throated Honeyeater, *M. albogularis* is the non-endemic member of the genus, with distribution extending from the Northern Coast of Australia, into Southern New Guinea (Longmore 1991). There has been some dispute as the validity of these six species, with some suggestion that *M. gularis gularis* (Black-chinned Honeyeater) and *M. gularis laetior* (Golden-backed Honeyeater) to be separate species (Longmore 1991). Both Slater *et al* (1997) and Pizzey and Knight (1997) consider *M. gularis* of comprising of two races, the nominate

Black-chinned Honeyeater (*M. g. gularis*), and race *M. g. laetior* (Golden-backed Honeyeater) in the Northern extremes of this species distribution. Keast (1968a) in his study of ecological niches within this genus defines six rather than seven species.

Feeding behaviour within this genus ranges from foliage or branch gleaners in the smaller species, to less specialized feeders in the larger species (Keast 1968b). This has allowed species of *Melithreptus* to be sympatric (commonly a larger and smaller species) (Keast 1968b). Tasmania's Melithreptids provide an extreme example of this. These two species (*M. affinis* and *M. validirostris*) co-exist to a greater extent than their mainland counterparts (Slater 1994).

Unlike other members of the Meliphagid family, the *Melithreptus* honeyeaters are thought to be more dependant on *Eucalyptus sp.*, than on other nectar-producing plants such as *Banksia sp.* and *Grevillea sp.* (Gannon 1966), which have traditionally been considered essential to honeyeaters if energy requirements are to be met (Ford & Paton 1976). Gannon (1966) suggested that this apparent dependence on *Eucalyptus sp.* may be a limiting factor with regards to the distribution of members of this genus, with all species being restricted to woodland habitats as opposed to heathland vegetation (Longmore 1991).

3.2.3 *Melithreptus affinis*

Melithreptus affinis was first described in 1835 by Jardine and Selby, though the current name was allocated by Lesson in 1839.

3.2.3.1 Description

M. affinis is a small honeyeater (family Meliphagidae), measuring between 12.5-14.5 cm in length (Pizzey & Knight 1997), and weight approximately 15g (HANZAB 2001). In plumage, no sexual dimorphism occurs between the sexes, though Brent (1905) suggests that the male is "a little brighter" (Brent 1905, pp. 13). The adult of the species is characterised by a completely black head and throat, bar a blue/white crescent above the eye. Distinctive black

shoulder bars are another distinguishing feature of the species. The wing and back of the bird are a dull olive-green, becoming brighter during the breeding season (pers. ob.). The belly/underside of the bird is white. Juveniles differ to the adults in plumage colour, with the head a patchy brown, the throat white/grey, and the shoulder bands absent. Bill and legs are also paler than in adults (See Plates 3.1 – 3.3).

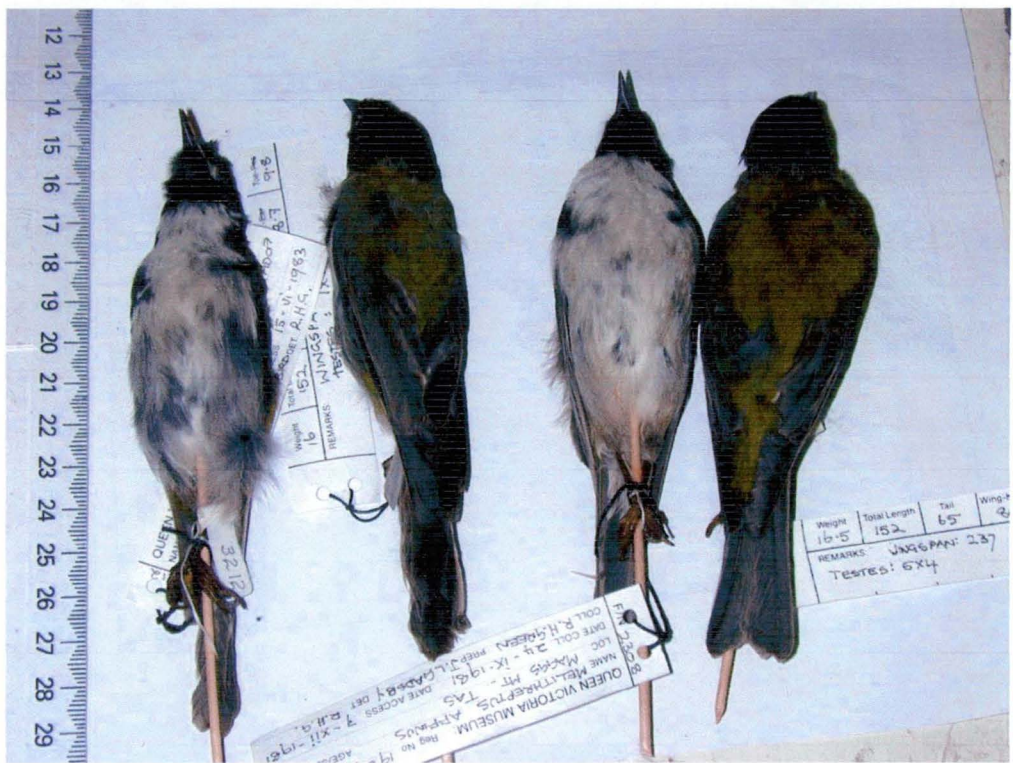


Plate 3.1 adult *M. affinis*, male

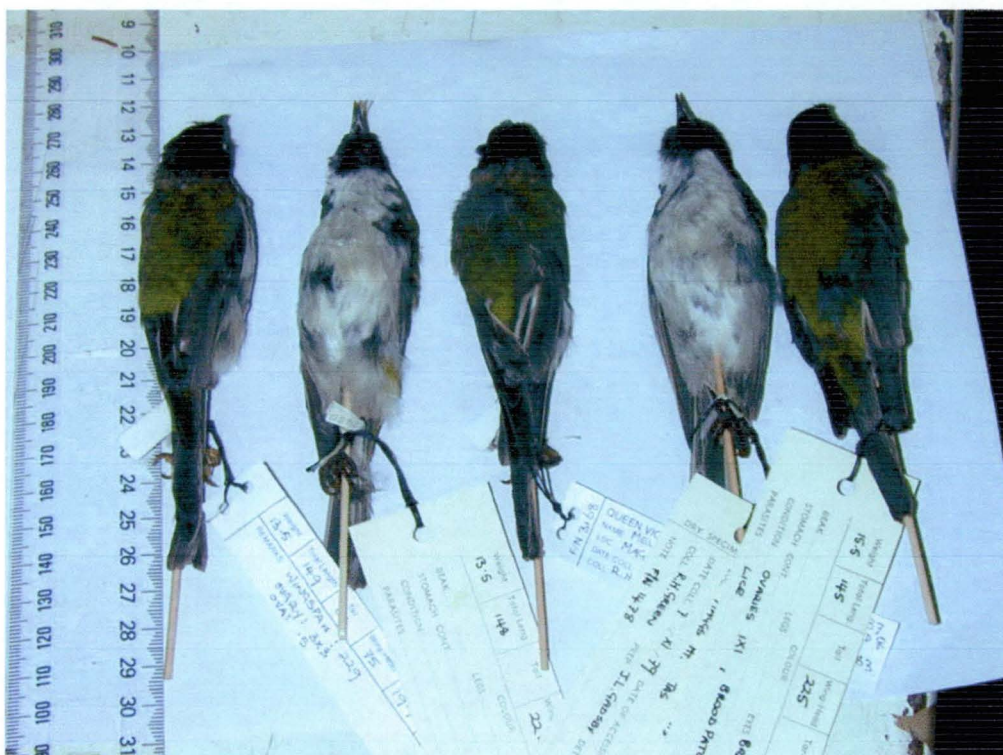


Plate 3.2 adult *M. affinis* female



Plate 3.3 juvenile and adult *M. affinis*

Morphological variations have been identified between the sexes. Males show significantly longer wing, tail and bill measurements than females (HANZAB 2001), though weights do not differ. Juveniles were found to possess significantly longer tails than adult birds, though wing length was significantly reduced (HANZAB 2001).

Compared to other members of the genus, *M. affinis* has a significantly reduced bill and hallux length than other members of the genus (Keast 1968a).

3.2.3.2 Distribution and Habitat.

M. affinis is endemic to Tasmania and surrounding islands (King Is., Flinders Is., Maria Is, Bruny Is.). On mainland Tasmania, the species is strongly orientated to the east of Tyler's line (Mesibov 1994; Green 1995), though the species is not unknown along the west coast around Strahan (Figure 3.1 from Thomas 1979).

Tyler's line divides Tasmania into two based on climatic, geological, edaphic and vegetational changes (Mesibov 1994). The west of the line is characterised by a much wetter climate on an older geology. This supports much of Tasmania's Temperate Rainforest and alpine regions. The east of the line is sandstone geology, dominated by *Eucalyptus* woodland/forest (Williams 1974).

M. affinis is typically found within Eucalypt woodland. There is also a selection for mature growth rather than young regrowth vegetation (Recher *et al.* 1971). Understorey of fairly dense shrub appears preferable, though individuals have been recorded across varying understorey types. The species is rarely encountered within urban environments.

Altitude is another factor thought to influence the species' distribution, with individuals generally found below 1000m asl. (subalpine/alpine observations have been noted up to 1200m asl) (Ratkowsky & Ratkowsky 1987). Green (1995) suggests that the species is confined to below 500m asl as habitat preferences are found across the lowlands of the state.

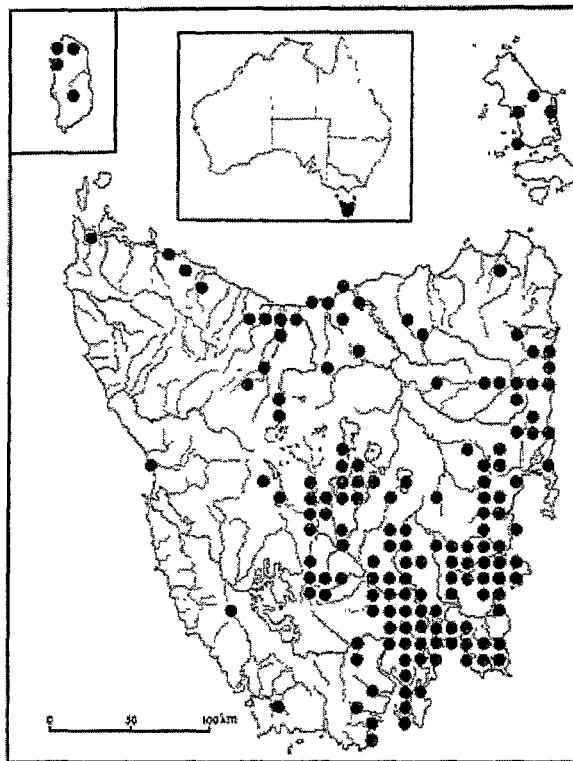


Figure 3.1. Distribution of *Melithreptus affinis* in Tasmania (from Thomas 1979).

3.2.3.3 Movements

No long term study has been undertaken on this aspect of *M. affinis*. What information available is based on incidental observation with varying opinion on the species movements. Green (1995) considers the species to be relatively sedentary, with local populations staying within an established range, as does Keast (1968a). Other authors, such as Slater (1994) and Thomas (1980) suggest the species is nomadic, following availability of food, a trait common in many of Australia's avifauna (Ford 1989).

3.2.3.4 Diet and Foraging behaviour.

As with Australian mainland members of the *Melithreptus* genus, *M. affinis* depends predominately on a diet of arthropods, even though possessing the brush tongue characteristic of the Meliphagidae family. Barker and Vestjens (1989) list fruit, and various arthropoda (Orthoptera, Hemiptera, Coleoptera,

Diptera, Lepidoptera, Hymenoptera and Arachnida) in their analysis of stomach contents of *M. affinis*. There was no evidence of nectar use. Whilst undertaking captive studies of the species, Green (1995) found that without protein supplements to food provided, individuals lost body condition rapidly, indicating the importance of protein in the diet of this species.

This supports evidence from the studies of Thomas (1980), and Slater (1994) both of whom considered microhabitat choice and feeding behaviours. *M. affinis* is generally found to feed in the upper canopy (76-93% of observations, Thomas 1980), gleaning insects off the foliage. Nectar appears to be of limited importance for the species; however, Cale (1994) considered the species to be nectarivorous as all feeding observations of the species were at nectar sources. This suggests an ability of the species to exploit resources whenever they become available, a characteristic common to other insular fauna (Keast 1970).

It is to be noted that species feeding within blossoms may not be taking nectar or other carbohydrate forms. McFarland (1984) considers the possibility that birds feeding on inflorescences may be taking the insects found to be feeding within the flower heads. This is possible as many of Australia's (and thus Tasmania's) native flora are insect pollinated, suggesting high insect abundances within inflorescences at times of flowering (McFarland 1984).

Other records suggest the species' diet to be more diverse, with Gannon (1962) suggesting that *M. affinis* forages on fruit, causing damage to orchards. The stomach contents of Museum Specimen no. B3846, held at the Tasmanian Museum and Art Gallery, was recorded as containing seeds when first preserved. The taking of fruit is supported by personal observations of the species. Anecdotal observations were made of an adult and juvenile *M. affinis* feeding on the fruit of a propagated plum tree in a suburban backyard. This was during the summer of 2003, and believed to be in response to the drought conditions of the time. Birds were being forced out of 'normal' habitats due to reduced water availability, and found in areas where they would not normally be located if food was readily available. Observations of this species foraging on *Exocarpus* sp. further indicates a frugivorous component to the diet. It was not clear whether individuals were taking fruit or feeding

on arthropods, but fruit may become a food supply when other resources are low,

3.2.3.4 Sociobiology

During the non-breeding period the species forms loose flocks of mated pairs, seasonal offspring and other adults (HANZAB 2001). Flock size can vary from a single pair to up to 30 birds (Slater 1994). Slater (1994) suggested a median flock size of 3 individuals. During the breeding period flocks break up into loosely formed colonies of nesting pairs. These pairs are thought to be monogamous, with the possibility that individuals pair for life (D. R. Milledge in HANZAB 2001). Co-operative breeding has also been recorded for this species. No records are available as to the territorial behaviour of this species during both the breeding and non-breeding seasons, though agonistic behaviour towards interspecific competitors has been frequently noted (Campbell 1903; Slater 1994).

3.2.3.5 Breeding Biology.

No scientific study has been undertaken on this aspect of the species' biology. Incidental observations suggest that breeding occurs from late September, early October through to December (HANZAB 2001).

Nest site is generally in the top of crowns or outer foliage of tree – predominately *Eucalyptus sp.* at an average height of 14.1 m (HANZAB 2001). Brent (1905) is one of few written records of this species breeding. From an observation of a single nest it is suggested that, after pairing, both male and female birds participate in nest building.

The nest is made mostly of bark, bound by spider web or silk from cocoons, incorporating various other materials such as grass, leaves, wool or hair (HANZAB 2001). The nest is lined with feathers, fur or other soft, fluffy fibres, including some plant seeds. Once completed, this structure measures approx. 4.76cm (± 0.37) across its internal diameter, and has a depth of 4.92cm (± 0.61) (HANZAB 2001).

It is unknown what time period occurs between the completion of nest and the laying of first eggs. Brent (1905) suggests it is within a week, though this being the only recorded observation, it is only a guide to this aspect of the species' biology. One record of a partially built nest had three fresh eggs in it 18 days later (HANZAB 2001).

No information is available on the laying period of the species or synchrony of hatching. Clutch size has been recorded as "usually three" (Brent 1905). Other sources (see Longmore 1991; HANZAB 2001) also suggest a clutch size of three. The Australian Nest Record scheme (which has been active since the mid 1960's) has no records for *M. affinis*.

Incubation period is estimated to be between 16 – 21 days (Longmore 1991; HANZAB 2001). There is some contention as to whether the female alone incubates, or the male helps. To add to this confusion, cooperative breeding has been recorded to occur within this species (HANZAB 2001; Cocheran pers.com.).

Once eggs have hatched, both parents have been recorded to feed nestlings. Other adults within communal groups will also help. It is held that a period of 15 days (Longmore 1991) lapses before young leave nest. The actual success rate of young for this species is not known. Parasitism by cuckoos (*Cuculus pallidus*, *Cacomantis flabelliformis* and *Chrysococcyx basalis*) has been recorded for the species.

3.2.3.6 Conclusion

The limited amount of research undertaken on *M. affinis* is apparent in the brevity of information incorporated in this chapter. With the research undertaken in this study, the aim is to begin to answer some of the questions encountered in even the most basic of life history traits of *M. affinis*.

M. affinis is a unique species, of limited distribution. It has potentially been exposed to extreme climatic and geological conditions (Ridpath & Moreau 1966). Understanding the ecology of this species will not only assist the long term survival of it, but potentially shed more light on the development of the avifauna of Australia.

3.3 Life History.

As previously discussed, the ecological knowledge of *M. affinis* is lacking at even the most basic level. The rest of this chapter is allocated to try to expand on the ecological data presented above. This will be done through the analysis of banding data obtained from the Australian Bird and Bat Banding Scheme (ABBBS). Though this data set is far from complete, some trends may be extrapolated. In addition, flock size and seasonal variations are also explored from data that was collected during this study.

Seven hundred and fifty banding records were obtained from the ABBBS and all inferences are made from this data. These records cover a period from 1965 through to 1992, and are distributed across most of the state of Tasmania. For a list of locations, bander, date and number of records see appendix 1. Banding data includes date of initial capture, location of capture, band number and age of birds. For some records, banders allocated age as adult or juvenile. In other instances banders allocated an age class to the netted birds. The age classes allocated by some banders have been used during analysis. This will cause some bias in the data as ages may have been inaccurately assigned. Gender has also been noted, though this is based more on behavioural observations than any other method. Morphological measurements of weight, tarsus length, bill, total head length, tail and wing length were recorded for a proportion of the records.

Of these 750 records, 16% of records are recaptures. General trends have been extrapolated from the data.

3.3.1 Longevity and survivorship

It is impossible to determine the structure of the population of this species from the banding data obtained. Age classes assigned to birds are vague at best. For some records, birds have been aged as simply adult or juveniles, whilst for other records birds are allocated an age group. The data that could be extracted has been used to develop a survivorship curve (figure 3.2). This figure presents a curve for all appropriate data. Two sites where sufficient banding records were available have also had a survivorship curve developed.

For both sites, a substantial decrease occurs in the cohorts between the first and second years. This decrease is consistent in combined data, with the mortality rate being uniform until the second year.

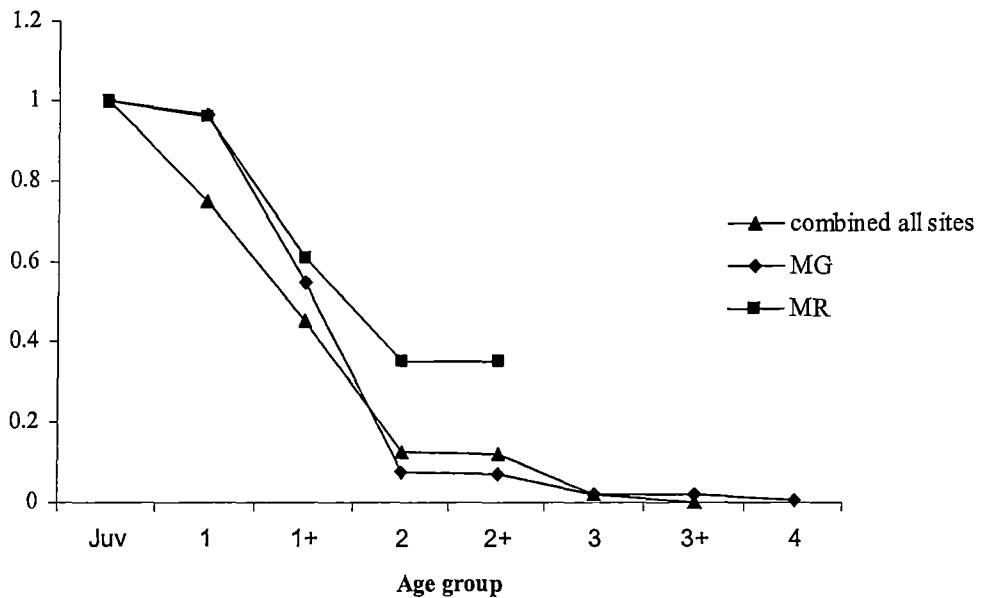


Figure 3.2 Approximate survivorship curve for *M. affinis* for the first 4 age cohorts. This figure is compiled from all banding data where individuals are allocated an age group. MG – Maggs Mountain, MR – Meehan Ranges. Data from ABBBS.

Increased longevity in Australian birds has been suggested as a life history trait adapted specifically for the environmental conditions faced by this group of birds. Thomas (1974) and Woinarski (1985a) both suggest that there is evidence for this life history trait, with Poiani and Jermin (1994) undertaking a comparative analysis of traits in Australian passerines. Their conclusions were in agreement.

M. affinis shows evidence of this characteristic. In 1972 D. R. Milledge caught and banded a bird, band number O21 – 03772. This bird was allocated an age class of 2+ at this time. This bird was re-caught in 1981, after a period of 8 yrs 7 months and 29 days, giving this bird an age of at least 10 years.

3.3.2 Population size

Species with small population sizes are susceptible to inbreeding depressions and are more sensitive to demographic instability and environmental change (Wilcox 1980 cited in Chapman 1995). *M. affinis* being confined to an island has ecological restraints placed upon it, and subsequently a finite population size. In an analysis of the historical data sets, two sites had sufficient data to make some inferences about the local population sizes, and determine the variation between years. Population estimates were calculated using the Jolly-Seber model (Seber 1986; Pollock *et al.* 1990). Trap times were allocated on a yearly basis, combining all trap records for that year. Figure 3.3a and b present the population estimates for Maggs Mountain (146° 12' E, 41° 31' S; records from Green) and Ridgeway (147° 17' E, 42° 56'S; records from Harris). Population estimates presented in figure 3.2a from Maggs Mountain in the north of the state shows a decline in the population between 1985 and 1986. This population decrease continues into 1987, with the population starting to recover in 1988. For Ridgeway (figure 3.2b), the population estimate is substantially smaller than that estimated for Maggs Mountain. The trend observed in this figure suggests that the population was fairly stable from 1977 through to 1979, with a decrease into 1980.

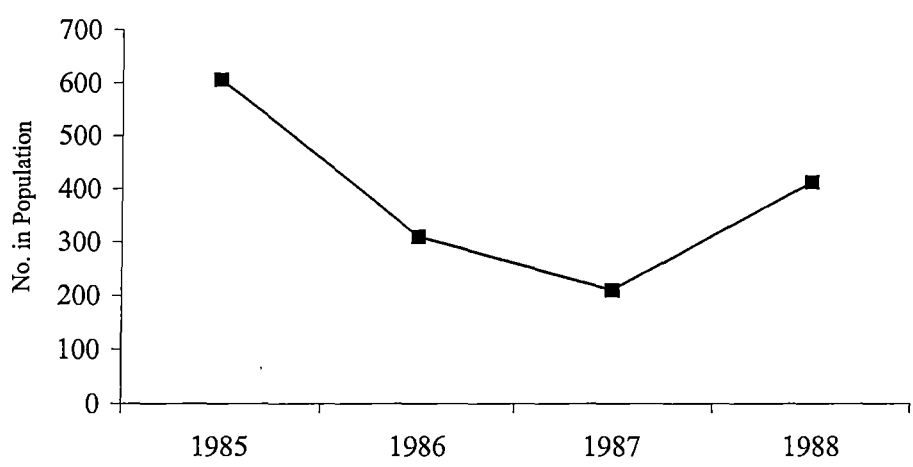


Figure 3.3a Population estimates for *M. affinis* at Maggs Mountain between 1985 and 1988.

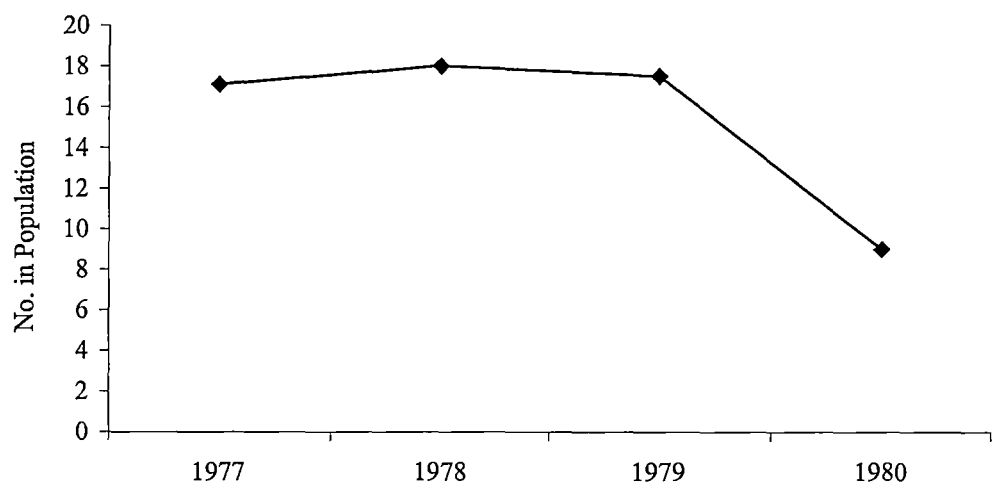


Figure 3.3b Population estimates for *M. affinis* at Ridgeway between 1977 and 1980

Though these results are historical and only estimates, they still allow for some general conclusions about *M. affinis*. The first point is that the populations are not stable. Like every other organism, the population fluctuates - in response to environmental condition, resource availability and a myriad of other constraints. For the Maggs Mountain population it can be seen that these fluctuations can be quite substantial. The population decreases by almost 50% between 1985 and 1986, with a recovery in numbers taking another two years.

This also shows that birds are distributed differently across different geographic regions. This is important in the management of the species, particularly if it ever becomes vulnerable or threatened, as local extinctions may be occurring, but the population be stable in other areas.

The differences in population size between the two sites are large. Maggs Mountain has a calculated population maximum of over 600 individual, whereas Ridgeway has a population of 17. This may be in part explained by the banding effort, as Maggs Mountain had 303 records compared to 108 records at Ridgeway. The area over which banding took place may also differ (this information is not available). The other factor influencing these population estimates is the season in which banding took place. The literature to date indicates that *M. affinis* is nomadic during the non-breeding period, thus the chances of locating and marking birds during this period decreases dramatically if birds are moving around. Of the records taken at Ridgeway, 77% were taken during the non-breeding period, so the chances of catching birds during this period were low, and the chances of recapture also decreased. Conversely, only 25% of records at Maggs Mountain are during the non-breeding period, so at this point the population is probably more stable, and much easier to locate, resulting in the higher population estimate. Personal observation suggests that birds will concentrate in small areas to breed, potentially causing the increase in population size calculated for Maggs Mountain. Slater (1994) stated that *M. affinis* is a colonial or semi-colonial breeder. Thus the population estimates at Ridgeway may be of residents during the non-breeding period, and Maggs Mountain records are those of

resident birds during the breeding period, which may incorporate individuals that would not be found in that area outside of the breeding season.

3.3.3 Movement patterns

Examination of the obtained banding records shows that only three birds were recaptured away from the site where they were originally banded. These 3 birds were found at Ridgeway, one month after their original banding at Tinderbox, a distance of approximately 15km. This group was made up of one adult with two juvenile birds, probably the offspring from that season's breeding, as records are December/January. All other recaptures recorded for *M. affinis* have been from the same site where the bird was originally banded. On average birds were recaptured after 9.77 months (S.E. 1.27months n = 120) after previous capture. These captures are distributed across both breeding and non-breeding periods.

Inferences about the movement patterns from this data are as follows:

- At least a section of the population are resident or locally nomadic in the vicinity of banding locations, with a small number of birds being recaptured at the same location during no-breeding periods
- There appears to be a strong breeding site tenacity.

Table 3. 2 presents data for five individuals captured four or more times. This table provides the time period elapsed between first and final record, the age class of the birds as well as location. This suggest that the birds numbered O22 – 13933, O22 – 13958, O22 – 23952 and O22 – 23983 are long term residents with captures over a period of years. Bird number O21 – 74704, may be resident, or is showing breeding site tenacity, returning in at least three consecutive years (1984-86) to the same location to breed. This appears to be a common occurrence, with the majority of initial captures and subsequent recaptures occurring during breeding periods.

The banding data suggests that a proportion of the population of *M. affinis* is sedentary during both breeding and non-breeding periods. However, the small percentage of recaptures supports the current literature that the species

is highly nomadic during the non-breeding period. This life history trait is common within other species of honeyeater (McFarland 1986a).

Table 3.2 periods of time elapsed between multiple recaptures. This data suggests that a proportion of the population of *M. affinis* is resident around trapping sites, with breeding site tenacity also being demonstrated.

| Bird No. | Location | Age class | Date of initial capture | Final recapture | Breeding or Non-breeding | No. of captures |
|-------------|-----------|-------------------|-------------------------|-----------------|---------------------------|-----------------|
| O21 - 74705 | Maggs Mt. | Adult | Sept. 1984 | Sept. 1986 | Breeding | 4 |
| O22 - 13933 | →Ridgeway | Juvenile Adult | March 1975 | June 1976 | Breeding and non-breeding | 4 |
| O22 - 13958 | →Ridgeway | Juvenile Adult | April 1975 | Sept. 1980 | Breeding and non-breeding | 6 |
| O22 - 23952 | →Ridgeway | Juvenile Adult | May 1976 | March 1979 | Breeding and non-breeding | 4 |
| O22 - 23983 | Ridgeway | Adult | May 1976 | May 1980 | Breeding and non-breeding | 6 |

3.3.4 Flock sizes

If *M. affinis* does disperse during non-breeding periods it would be expected that there would be significant variation in flock sizes between breeding and non-breeding periods. Slater (1994) found a statistically significant increase in flock size between the breeding season (flock size 2.0, range 1-8) and non-breeding season (flock size 3.0, range 1-8).

Data was collected on flock sizes between August 2000 and November 2002. This included the number of adults and juveniles within each flock. Average flock size during the breeding period were 3.93 (range = 2-8, n=58), and non-breeding were 5.26 (range =2-20, n=32). Using Kruskal-Wallis non-parametric ANOVA, these variations in flock size were found to be significantly different (Chi = 4.324, d.f.=1, p=0.038). When considering age groups of birds, average flock size during the breeding period for adults was 3.24 (ranging 2-8, n=58) and juveniles 0.69 (range= 0-3, n=58).

Flocks recorded during the breeding period, are not necessarily indicative of the size of breeding groups. Observations suggested that although pairs (and

in some instances communal groups) will separate to nest, and defend a territory, general feeding areas are still utilised by all birds. At one site in the current study, birds were generally found feeding along a creekline in larger groups, and then breeding group's would return to nest sites.

The other point to note is the climatic conditions during the period of data collection. Through the breeding period of this study, much of the region was drier than average (see chapter 2), potentially forcing birds to forage in the most productive areas (eg along creek line) when, under "normal" conditions this flocking may not occur, as the food resources are not as concentrated

3.3.5 Conclusion

The analysis of these banding records allows a greater understanding of general life history parameters for *M. affinis*.

What these records suggest are:

- high mortality in the first couple of years;
- longevity similar to mainland avian species;
- variation in population size with location and season;
- breeding site tenacity; and
- fluctuations between breeding and non-breeding in flock size.

This is an initial step in determining the basic ecological characteristics of a unique, insular bird. It is, however far from a complete picture, and further studies will need to be undertaken.

4. SEASONAL AND CLIMATIC INFLUENCES ON THE FORAGING AND TIME BUDGET OF THE BLACK-HEADED HONEYEATER (MELITHREPTUS AFFINIS) IN TASMANIA, AUSTRALIA.

Abstract

Melithreptus affinis is a small honeyeater, found only in Tasmania, Australia. Observations were made of general behaviours and foraging methods in order to construct a time budget for the species over the period 2000-2002. Data were tested to determine if season, breeding period or diurnal period influenced the behaviour of the species. These test variables showed varying impact on the behavioural time budget of the study species, with most variation attributed to the environmental conditions encountered over the study period. During the study period, the first twelve months received substantially less rainfall than average, causing drought conditions. The second twelve month period received above average rainfall. Behavioural changes corresponded strongly with these changing climatic conditions. Seasonal, breeding and diurnal variations were observed in the foraging method employed by the species. Again, foraging changed in response to climatic variation.

4.1 Introduction

The variation in behaviours of an avian species is thought to be attributed in part to simple functional responses associated with variations in local environments (Carrascal *et al.* 1994). However, to understand these responses one must first be aware of how individuals use their environment, and how this utilisation relates to temporal and spatial patterns in the distribution of resources and other factors (Pyke & O' Connor 1993).

Limited research has been undertaken on much of Tasmania's avifauna, though the island supports twelve endemic species, and faces pressures similar to other areas of the continent. Like much of the Australian mainland, Tasmania's native woodlands are not adequately reserved (Mendel & Kirkpatrick 2002), leaving them exposed to future clearing. This will have implications for avifauna that inhabit these areas. Currently, habitat loss is considered the foremost threatening process to Australia's woodland birds (Olsen *et al.* 2003). Also, due to both biogeographical and geological influences, adaptations of organisms in Tasmania may differ from those in other areas of Australia.

Niche theory predicts that a species, found on an island that supports a subset of a mainland community, will have a larger realized niche than conspecifics on the mainland (Wright 1980). The Black-headed Honeyeater *Melithreptus affinis* (family Meliphagidae) is the smallest (130-150mm, 14-16g) of the 10 species of honeyeater found in Tasmania. It is endemic to Tasmania and the Bass Strait Islands (King Island and Furneaux Group).

Keast (1968a) suggested that this species of honeyeater is very “warbler like” in its morphology, indicating different habits to other members of the family. This appears so with regard to its feeding niche. Though the species is a member of the Meliphagid family, its diet is predominately insectivorous (Thomas 1980; Slater 1994), reflecting the abundance of this resource in Tasmania compared to other food (Ridpath & Moreau 1966). Thus it is a honeyeater that is not really a honeyeater. There is evidence that the species is able to exploit nectar resources when available, as defined by Cale (1994), who did not include *M. affinis* in a study of Tasmanian insectivorous birds. The dependence on arthropods as a major food source for *M. affinis* suggests that a strong association between foraging behaviour of the species and insect abundance should be seen. Subsequently, external factors that affect arthropod abundance will indirectly influence foraging and other behaviours of this bird.

Numerous studies in Australian forests and woodlands have suggested that rainfall affects the abundance of arthropods present in both canopy and understorey vegetation (Bell, 1985a; Frith, & Frith 1985; Abbott *et al.* 1992; Recher *et al.* 1996). Bell (1985a) found a change in arthropod abundance ratio from 10:1 to 2:1 (Summer maxima: winter minimum) in New South Wales during drought conditions. Similar abundance ratios were calculated by Abbott *et al.* (1992), again showing a major decline in the abundance of arthropods as a result of drought.

During the period of the present study, the field sites used experienced below average rainfall, and although similar arthropod data is not available for these sites, it can be inferred from other studies that this will cause a decrease in the abundance of arthropods available for insectivorous birds to feed upon. Thus it should cause variation in the foraging and behaviour of *M. affinis*.

The aim of this study was to quantify the behaviour of *M. affinis* and construct breeding and non-breeding time budgets for the species. These were tested to determine if differences occurred in the time allocated to behaviours, and foraging method over these periods. Season or diurnal period were also explored to determine if effects occurred on the time allocated to particular behaviours. There was a desire also to determine if these periods influenced the foraging activities of the study species. The implications of drought and subsequent resource availability were also considered.

4.2 Methods

4.2.1 Study Area

Field sites were located across the greater Hobart area, on both the eastern and western sides on the Derwent River. Sites were selected for two main reasons. These were:

1. *M. affinis* was consistently encountered at the site all year round,
2. The vegetation types were consistent across all sites.

The major vegetation types sampled have been defined by North (1997; 2000) as DRY-gPULC *Eucalyptus pulchella* grassy woodland, DRY-shPULC – *E. pulchella* shrubby forest and DRY –shOB – Shrubby *E. obliqua* dry sclerophyll forest.

DRY-gPULC *Eucalyptus pulchella* grassy woodland is a community occupying well drained slopes on dolerite. *E. viminalis* and *E. globulus* are often co-dominant with *E. pulchella*. Understorey vegetation tends to be a scattered shrub layer of *Busaria spinosa*, *Dodonaea viscosa*, *Acacia dealbata*, *A. mearnsii* and *Exocarpus cupressoides*. Grasses are dominated by *Poa rodwayi* and *Themeda triandra* (North 1997; 2000).

DRY-shPULC – *E. pulchella* shrubby forest supports a similar array of plant species to the above described vegetation type. Other *Eucalypt* sp. are not co-dominant however (North 1997; 2000).

DRY –shOB – Shrubby *E. obliqua* dry sclerophyll forest. This vegetation type is interspersed throughout the above described vegetation types, occupying areas of higher moisture content. It is typical of areas which would support wet forests if a reduction in the incidence of fire regime occurred. Prominent understorey plants include *Bedfordia salicina*, *A. verticulata*, *A. melanoxylon*, *Pultenaea daphnoides* and *Goodenia ovata* (North, 1997; 2000).

Ridgeway Reserve

Ridgeway Reserve is located approximately 3km from the central business district of Hobart. The reserve is managed by Hobart City Council, and is a major water catchment site for the Browns River (Elton 1997). The two main sources of Hobart's water supply – Ridgeway Reservoir and the Waterworks Reservoirs are also located within the Reserve. The reserve covers an area of approximately 500 hectares (Elton 1997) Typical land use is for water catchment, grazing and recreation (Davies 1988).

For the purposes of this study, Ridgeway Reserve was separated into two distinct sites, located approximately one kilometre from each other. Site RW (42° 55' 30'', 147° 17') was located at the higher altitude (400 – 500m asl). This area is in close proximity to the townships of Ridgeway and Ferntree and shows varying degrees of disturbance. Areas have been cleared for recreational use, as well as large corridors cleared under power lines. Areas have an understorey dominated by the introduced Gorse (*Ulex europaeus*) and as such are exposed to ongoing weed management, in the form of constant bulldozing of the weed infestation.

Site RR (42° 55', 147° 17' 30'') is located within the reserve, but closer to Hobart, with a lower elevation (300 - 350m asl). This site includes the vegetation proximal to the Ridgeway Reservoir which was built in the 1880's. This area of vegetation was most recently subjected to fire in 1998 and as such supports a different structural habitat to that of site RW.

University Reserve

This reserve is situated on Mount Nelson (42° 55', 147° 19'; 200-220m asl) and encompasses approximately 83 ha. The site is managed by the University of Tasmania, with the northern section allocated to sports fields. The rest of the reserve is used for teaching and recreational purposes. The site was most recently subjected to fire in 1995.

Knocklofty Reserve

Knocklofty Reserve is a bushland park 122ha in size (Knocklofty Reserve Fire management plan 1998). It is comprised of the slopes and the summit of Knocklofty, a prominent hill on the outskirts of Hobart (42° 53', 147° 18'; altitude 100m – 374m asl). Adjoining land use to the reserve include residential areas and an abandoned quarry to the north, residential areas to the east, and bushland (privately owned and council land), landfill sites and bushland reserves to the south and west. These tracts of bushland connect the reserve to Wellington Park (Knocklofty Reserve Fire Management Plan 1998).

The area supports vegetation comprising of wet forest along the lower south-facing slopes, dry grassy woodlands and grasslands. It was last burnt in 1993.

These sites are all located on the western side of the Derwent River. They are all relatively large, minimally disturbed areas, interlinked with Wellington Park, a 18 250ha reserve encompassing Mount Wellington and surrounding bushland

Meehan Ranges Recreational Reserve

The Meehan Ranges is a geological feature that runs approximately 14km along the eastern side of the Derwent River. It extends from Brighton in the north (42° 42', 147° 16') as far south as Rokeby (42°54', 147° 28'). Field studies have taken place towards the south end of the ranges near Cambridge, 15km east of Hobart (42° 50' 30'', 147° 24'). The area utilised for field studies has been declared a nature reserve. However, this reservation status tends to be overlooked, and the area is highly impacted upon by both motorcycles and bicycles along the creek line. Approximately a 1km x 1km section of the range was used during this study.

The vegetation of the study site varies as a permanent creek (Barilla Rivulet) runs through the centre of the study area. Canopy vegetation along the creek consists generally of *E. globulus*, *E. obliqua* and *E. rubida*. Further back as the slope steepens the canopy is dominated by *E. viminalis* with sporadic *E. pulchella*. Patches of the locally endemic *E. risdonii* also occur throughout this area, along with stand of *Allocasurinea* sp. Understorey is dominated by *Exocarpus cupressiformis* and *A. dealbata*.

4.2.2 Data Collection.

Data was collected opportunistically from September 2000 to August 2002. This encompassed two breeding and two non-breeding seasons.

Only adult birds were sampled. Birds were located by either sight or call. Once an individual was located for observation it was observed until a change in behaviour occurred from that originally encountered. This was to reduce the risk of biasing data towards obvious behaviours.

Observations during the breeding season were not taken directly around nests (though interactions at nests were recorded if they subsequently occurred during the observation period), as it was general behaviours, not specific breeding behaviours that were of interest in this particular study. Both breeding and non-breeding birds were potentially sampled, as individual birds were not distinguishable.

Individuals were watched for as long as possible, ending if a bird was lost at any time from the observer's view.

To ensure that samples were independent, once an individual had been lost

from sight it was not re-sampled. In instances where flocks were sampled, the next observed bird was selected at a distance from where the last individual was located and only those individuals where the observed was definite that they had not already been sampled were used. This meant that in cases of flocks of 4 or more birds, only a proportion of the flock was sampled.

Observations consisted of the focal individual being followed with behaviours being vocally recorded onto a hand held SONY® V.O.R microcassette – recorder M-530V, into which the observer recorded a continuous description of the behaviour.

Behaviour was allocated to one of nine categories:

- Glean (GL): When bird was seen to be searching out and feeding within the foliage, on the foliage.
- Probe (PB): This category included all observations of individuals when feeding on trunk or branches of a tree. This included probing under bark as a method of obtaining food as well as feeding directly off the trunk of the tree. It is possible that feeding on manna was occurring.
- Fly (FL): When individual was in the air. This included when birds moved between Branches whilst feeding. This was recorded as both the time spent flying plus an estimate of the distance flown.
- Perch (PE). This behaviour was allocated when an individual was stationary
- Preen (PR): This behaviour was allocated when individual was observed to demonstrate any type of grooming.
- Interspecific/Intraspecific Interaction (IA): Any interaction with other birds was recorded, including the species of bird and whether or not the focal species was the aggressor or on the receiving end of an attack.
- Move (MV): This behaviour was allocated to an individual when it was moving throughout the vegetation but not actively feeding.

- Nectar (NE): this category encompassed all observations of individuals feeding within blossoms.
- Hawk (HW): This behaviour was recorded when an individual was observed taking prey on the wing.

Total foraging time was calculated by combining glean, probe and nectar.

Records were transcribed from recorded vocal observations. This was done in a way as to determine 'real time' observations, where behaviours were timed with a Sportline® Watertight stopwatch to the nearest 0.1 of a second. The total time spent demonstrating individual behaviours were collated from these records (Oliver, 1998). This method was selected rather than instantaneous sequential methods (Recher & Gebski, 1990) as instantaneous methods tend to provide a representation of the frequency with which a behaviour is displayed rather than the duration of behaviour, and statistical comparisons on the data presented in this paper suggested that instantaneous observation only accurately reflect common, enduring behaviours (such as foraging and perching). Common, short-term behaviours (such as flight) and uncommon, enduring behaviours (eg. preening) tended to be overestimated in instantaneous sampling.

For analysis, the collated data were divided in three ways: to compare breeding seasons with non-breeding behaviour, to compare seasonal (summer, autumn, winter, spring) behavioural changes and to consider diurnal changes in behaviour.

Breeding season encompassed September through to February, with non-breeding encompassing the remaining six-month period. This division into seasons was based on observations of breeding behaviours and juvenile location over the study period. Signs of breeding such as displaying and courtship feeding were used as indicators of the beginning of breeding, with end of season being considered the end of February when juveniles were no longer apparent. Two breeding seasons; 2000 – 2001 and 2001-2002 breeding seasons and two non-breeding season of 2001 and 2002 were analysed. Seasons was separated based on standard divisions of 3 monthly increments.

Diurnal periods used for analysis were defined based on the angle of the sun (azimuth). It was decided to partition data up in this way to take into account the variation in day length between solstices. Being at a higher latitude than the mainland of Australia, Tasmania has greater variation in the length of daylight than other areas of the continent, and as all data were combined (both summer extremes and winter extremes) a method was needed to determine diurnal periods that would take into account the variation in day length. Diurnal periods were determined using 45 degree increments, with diurnal period one being early morning through to period four being late afternoon/sunset. The azimuth calculations used an online program provided by the Astronomical Applications Department of the U.S Naval Observatory, located at:

<http://aa.usno.navy.mil>.

Four diurnal periods were defined based on the azimuth measurements. These have been labelled diurnal periods one through to four, with one being early morning to mid morning (sun angle $45^{\circ} < \text{angle} < 90^{\circ}$), two mid morning to midday (sun angle between $0^{\circ} < \text{angle} < 45^{\circ}$), three midday to mid afternoon (sun angle $315^{\circ} < \text{angle} < 360^{\circ}$) and four being mid afternoon/sunset (sun angle $< 315^{\circ}$).

Climatic data were obtained from the Bureau of Meteorology from three weather stations. These stations corresponded as closely with field sites as possible. A proportion of the long-term average was calculated for each site over each breeding and non-breeding period.

4.2.3 Statistical Analysis.

As data collected was proportional it was first transformed using an Arcsin transformation (Zarr, 1999). The Freeman and Tukey (1950 cited in Zarr, 1999) transformation was applied (equation 1).

$$p' = \frac{1}{2} [\arcsin\sqrt{X/n+1} + \arcsin\sqrt{X+1/n+1}] \text{ (equation 1)}$$

This transformation was used as much of the data was at extreme ends of the range (ie near 0 or 100%) (Zarr, 1999).

Multivariate analysis of variance (MANOVA) was used to compare six behavioural groups (flight, forage, move, perch, preen and inter/intraspecific interactions) across the four time periods (breeding and Non-breeding, season and diurnal periods). This data was tested for univariate and multivariate normality, linearity and multicollinearity and found not to violate any assumptions necessary when undertaking MANOVA. Significance values were at 0.05. Tukey post hoc tests were used to determine where significant differences lay.

Foraging behaviours (Glean, probe and nectar) were calculated as the proportion of the total foraging time birds displayed feeding behaviour. This data was also tested for univariate and multivariate normality, linearity and multicollinearity and found to violate the necessary assumption for both analysis of variance (ANOVA) and MANOVA use. These analyses were undertaken using Non-parametric Kruskal-Wallis ANOVA, Wilcoxon Signed Rank test and Mann-Whitney U test. Where multiple tests were undertaken on this data, Bonferroni adjusted alpha levels ($\alpha = 0.008$) were used to reduce the risk of type one errors.

All statistical procedures were undertaken using SPSS 10.0 computer software.

4.3 Results

A total of 389 individual observations were recorded. Observations ranged in duration from 5 sec to 740 secs (mean \pm s.e. = 69 ± 4 secs).

Figure 4.1 provides seasonal rainfall across study sites as a percent of average seasonal rainfall for sites. This includes the non-breeding season before the commencement of the current study to allow for lag effects on resources. Substantial changes can be seen between seasons, with periods of drought experienced during the initial stages of the study. Also provided in this figure are monthly rainfall averages.

4.3.1 Breeding season versus non-breeding time budget.

Data was divided into breeding and non-breeding periods to determine if this influenced the time budget of the study species. Figure 4.2a shows the proportion of time allocated by individuals across 6 'common' behaviours ($n \geq 30$). No significant differences were seen between breeding and non-breeding seasons in five of these behaviours. The exception to this is in the proportion of time allocated to general movements through the vegetation, with a significant increase in time during the non-breeding season ($F_{1, 388} = 31.52, p < 0.001$).

With regards to the foraging of the species for breeding and non-breeding periods (Figure 4.2b), gleaning was the most significant feeding method employed by *M. affinis* ($Z = -8.356, p < 0.001$). The proportion of time allocated to probing behaviour significantly increased in the non-breeding season ($\chi^2 = 4.966, \text{d.f.} = 1, p = 0.026$).

The lack of variation in time budget between breeding and non-breeding season is further evident when data is divided into four annual breeding and non-breeding seasons (Figure 4.3a). At this level of analysis, significant differences were found to occur between years, rather than between breeding and consecutive non-breeding period. As seen in figure 4.2a, behaviours displayed by *M. affinis* during breeding season and consecutive non-breeding season (ie breeding 2000 – 01, and non-breeding 2001, breeding 2001-02 and non-breeding 2002) were not found to significantly vary. It is when comparing breeding season with breeding season and non-breeding season with non-breeding season that significant differences are seen occurring.

Time spent foraging was found to differ significantly ($F_{3, 388} = 8.411, p < 0.001$). *Post hoc* tests showed that breeding season 2000-01 significantly varied from breeding season 2001-02 ($p = 0.005$) as well as the non-breeding period of 2002 ($p = 0.001$). The non-breeding period of 2001 also shows this trend, with significant differences to breeding period 2001-02 ($p = 0.032$) and non-breeding period 2002 ($p = 0.001$). A similar trend can be seen in the

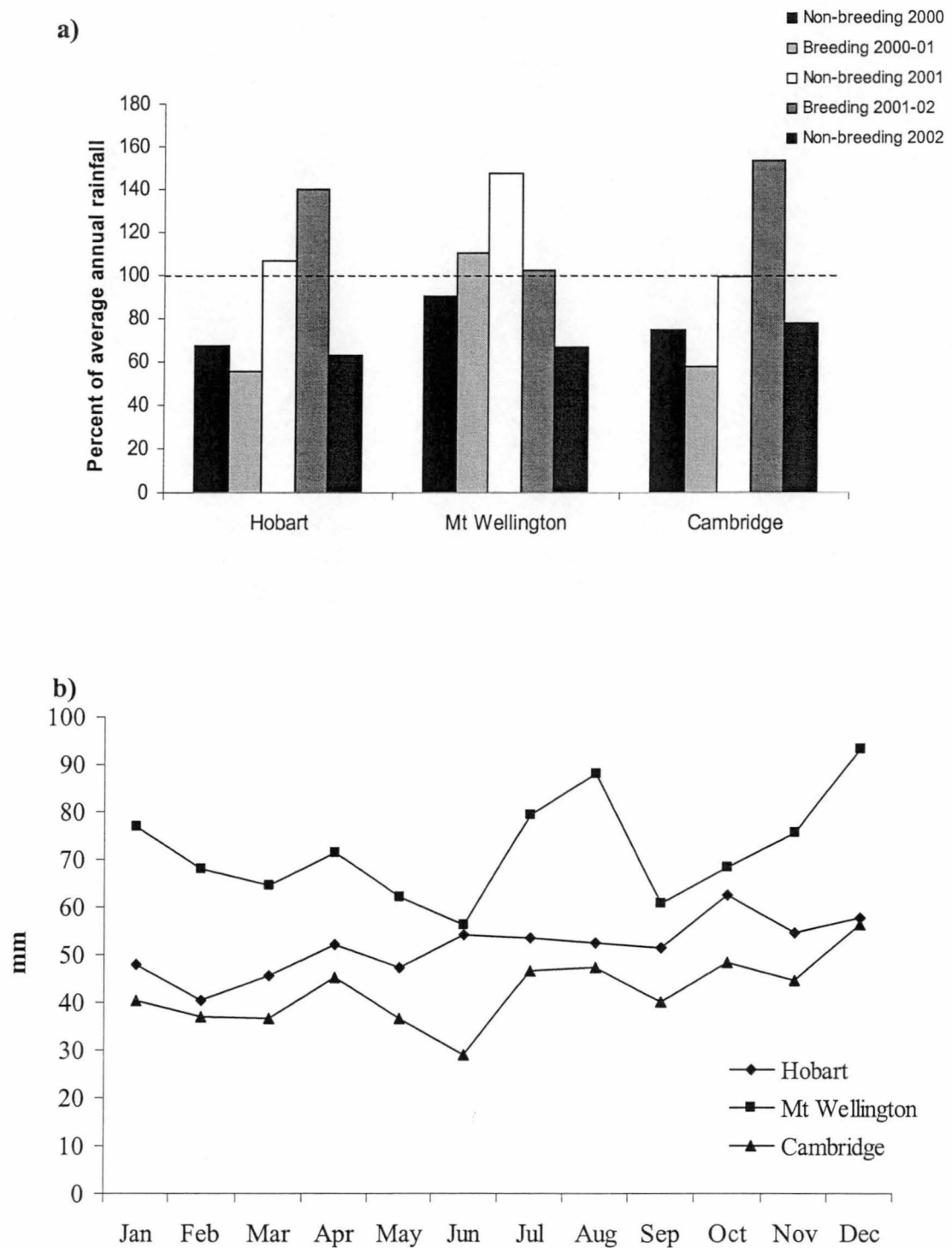


Figure 4.1 a) Percent of annual average rainfall encountered at major climate station during study period. Dotted line indicates 100% of annual average rainfall. b) Annual average monthly rainfall for major weather stations across study period.

proportion of time individuals spent inactive or perching ($F_{3, 388} = 4.968$, $p = 0.002$). Breeding 2000-01 and non-breeding 2001 were not significantly different to one another, but both showed significant differences to breeding 2001-02 and non-breeding 2002 ($p = 0.003$, $p = 0.032$, $p = 0.032$ and $p = 0.01$ consecutively).

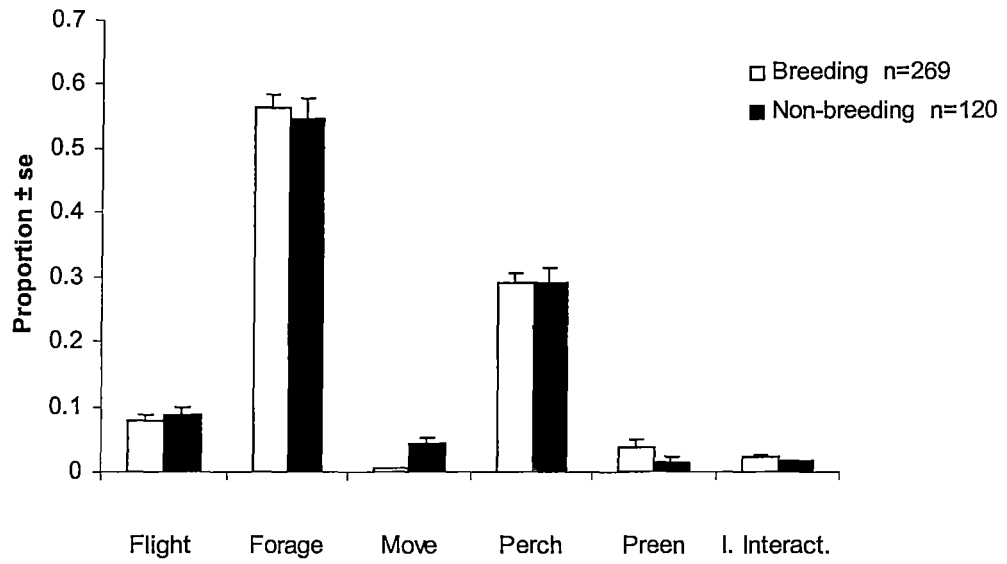
Variations in the proportion of time spent engaging in inter/intraspecific activities ($F_{3, 388} = 3.899$, $p = 0.009$), moving ($F_{3, 388} = 57.200$, $p < 0.001$), and flight ($F_{3, 388} = 3.474$, $p = 0.002$) were also found to significantly change with breeding and non-breeding periods. Inter/intraspecific interactions significantly varied between the two breeding seasons ($p = 0.004$), with a greater proportion on time spent interacting in the second season.

Movement significantly increased in the second non-breeding season compared to all other seasons (breeding 2000-01, $p < 0.001$; non breeding 2001, $p < 0.001$; breeding 2001-02, $p < 0.001$). Time moving in the second breeding season also showed a significant increase when compared with the first breeding period ($p < 0.001$) and non-breeding period 2001 ($p = 0.021$). Flight varied between the first breeding period (breeding 2000-01) and subsequent non-breeding period ($p = 0.034$).

It was desirable to consider the implications of breeding periods on the foraging method used by *M. affinis*. Time spent gleaning was found to differ significantly across breeding periods ($\chi^2 = 10.465$, d.f. = 3, $p = 0.015$).

Proportion of time spent probing also differed significantly across seasons ($\chi^2 = 12.941$, d.f.=3, $p = 0.005$). Nectar use was limited to the first breeding period, reflecting the lack of flowering in the *Eucalyptus sp.* across the study period. Though presented on figures, nectar use was not tested due to the limited number of observations. Table 4.1 shows the significant variations between breeding periods with regards to foraging behaviour.

a)



b)

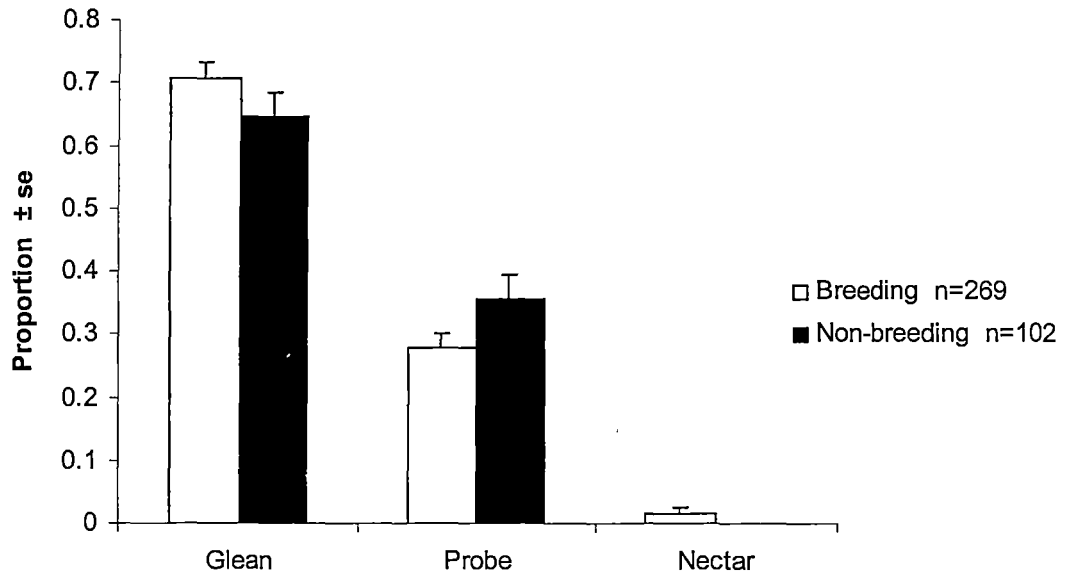


Figure 4.2 a) Time budget comparison between breeding and non-breeding behaviours in *M. affinis*. Data is given as the average proportion of time individuals engaged in behavioural categories \pm se. b) Foraging behaviour comparison between breeding and non-breeding behaviours in *M. affinis*. Data is given as the average proportion of time individuals engaged in behavioural categories.

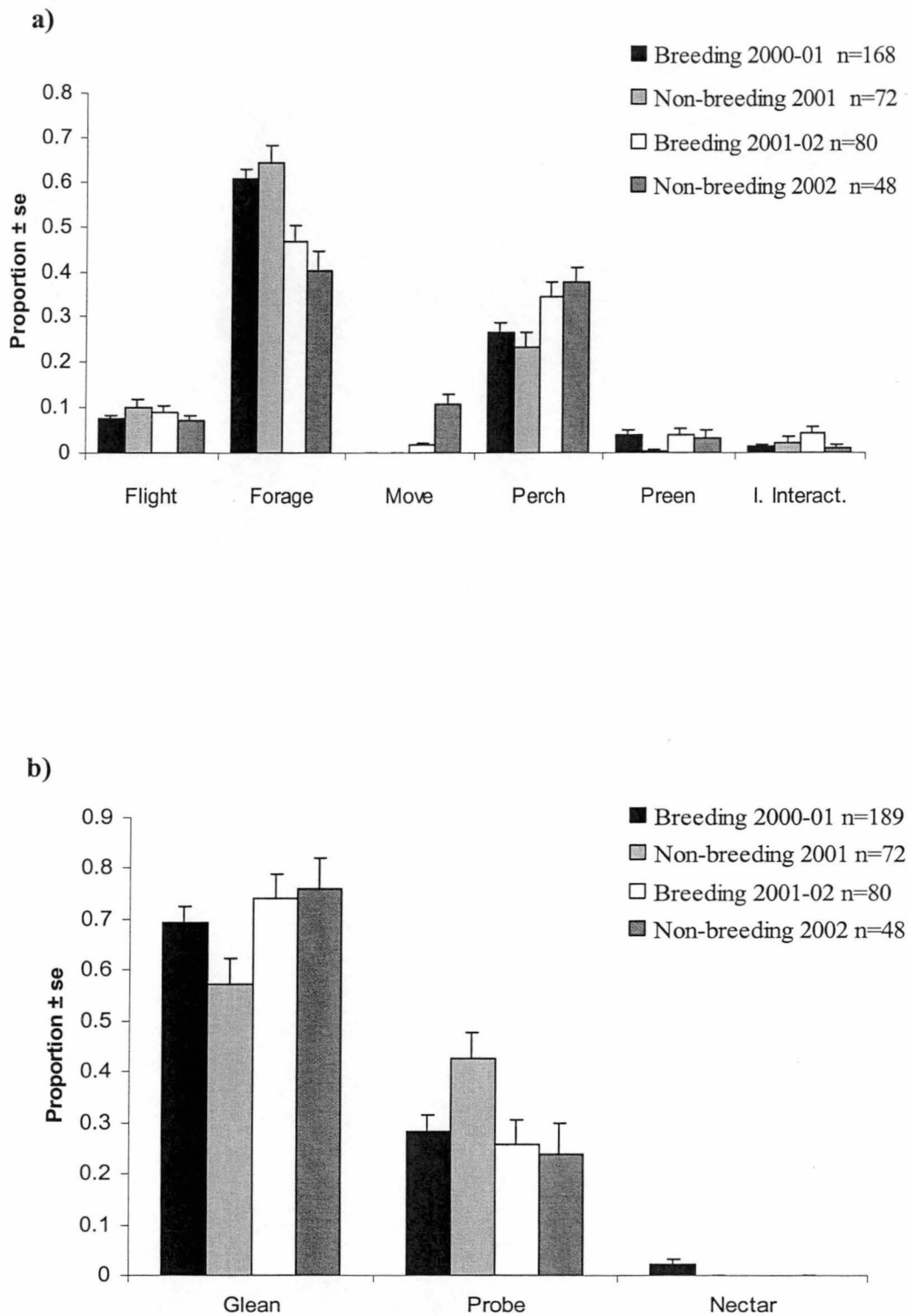


Figure 4.3 a) Comparison of time budget across four different breeding periods; two breeding seasons (Sept-Feb) and two non-breeding seasons (Mar – Aug). Data is presented as the proportion of total time \pm se for each of the behavioural categories. **b)** Comparison of foraging method across the four different seasons; two breeding seasons (Sept-Feb) and two non-breeding seasons (Mar – Aug).

Table 4.1 Mann-Whitney U test results showing where significant differences occur between breeding and non-breeding periods. $P<0.01^*$, $P<0.005^{}$, $P<0.001^{***}$ ($\alpha=0.008$).**

| | Br 00-01 | | NBr 01 | | Br 01-02 | |
|----------|----------|----------|---------|---------|----------|----|
| | GL | PR | GL | PR | GL | PR |
| Br 00-01 | - | - | - | - | - | - |
| NBr 01 | -2.859* | -3.334** | - | - | - | - |
| Br 01-02 | NS | NS | NS | NS | - | - |
| NBr 02 | NS | NS | -2.708* | -2.708* | NS | NS |

Statistically, gleaning was the significantly prominent feeding method (when compared with probing) for breeding 2000-01 ($p<0.001$, $Z=-6.589$), breeding 2001-02 ($p<0.001$, $Z=-4.008$) and non-breeding 2002 ($p<0.001$, $Z=-3.751$). There was no significant difference in the proportion of time spent gleaning or probing for non-breeding 2001.

4.3.2 Seasonal Variation

In a comparison across seasons (Figure 4.4a), no significant differences were observed in the allocation of time to foraging, perching, preening, flight and interaction. The time allocated by *M. affinis* to moving throughout the canopy did show significant variation ($F_{3,388} = 13.990$, $p<0.001$).

When comparing foraging behaviours across seasons, time spent gleaning and probing showed no significant differences between Summer and Autumn (Fig

5.4b), or Spring and Winter. Significantly less time was spent foraging in the canopy (glean) in winter than in summer ($Z = -5.568$, $p < 0.001$) and Autumn ($Z = -4.94$, $p < 0.001$). A significant decrease in this behaviour between Spring and Summer ($Z = -3.885$, $p < 0.001$) and Spring and Autumn ($Z = -3.309$, $p = 0.001$) was also encountered. Similar trends were found when considering time spent probing. Winter showed a significantly greater amount of time spent feeding with this method than in all other seasons (Spring, $Z = -3.019$, $p = 0.003$; Summer $Z = -5.571$, $p < 0.001$; Autumn $Z = -4.940$, $p < 0.001$). Spring was also significantly greater than Summer ($Z = -3.3169$, $p < 0.001$) and Autumn ($Z = -2.864$, $p = 0.004$) (Bonferonni adjusted $\alpha = 0.008$).

Hawking was not considered an important foraging method for *M. affinis*. Of 389 observations, a total of 19 hawking observations by 14 individual birds were recorded over the total data collection.

4.3.3 Diurnal Variations

As with season and breeding and non-breeding periods, the same six behavioural categories were considered over four diurnal periods. Figure 4.5a shows the proportions of behaviours with diurnal period. Much fluctuation can be seen in foraging and perching between diurnal groups. Five of the six behaviours were found to vary significantly with diurnal period. These were flight ($F_{3,388} = 3.185$, $p = 0.024$), forage ($F_{3,388} = 7.532$, $p < 0.001$), move ($F_{3,388} = 51.298$, d.f.=3, $p < 0.001$), perch ($F_{3,388} = 5.007$, $p = 0.002$) and inter/intraspecific interactions ($F_{3,388} = 4.713$, $p = 0.003$).

Table 4.2 provides results of *post hoc* tests. Foraging showed significant differences between morning and afternoon groups, as did perch. The time allocated to moving was significantly greater in the late afternoon.

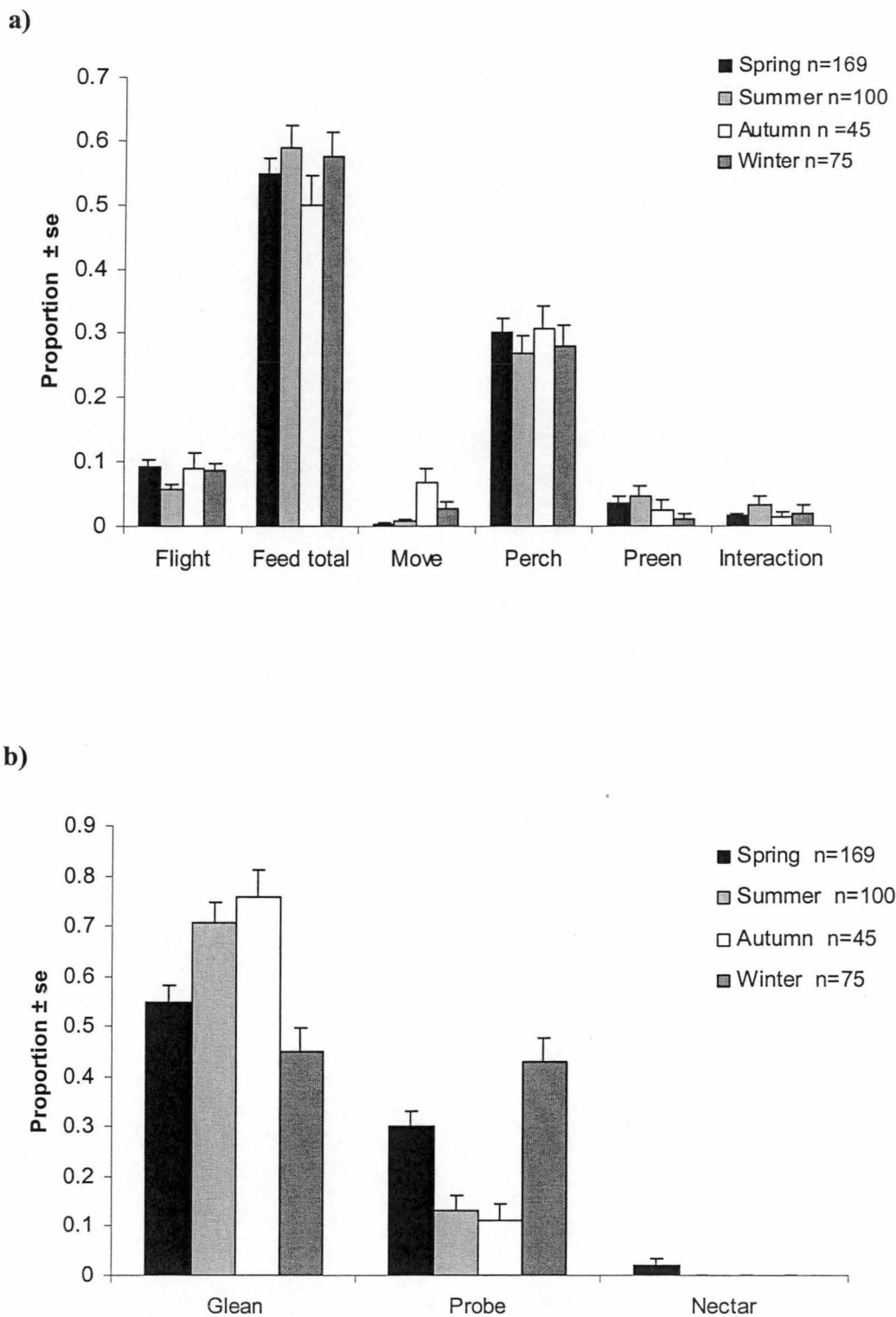


Figure 4.4 a) Time budget over season. Data is presented as a proportion of total time \pm se for each of the behavioural categories. b) Variation in foraging methods with season.

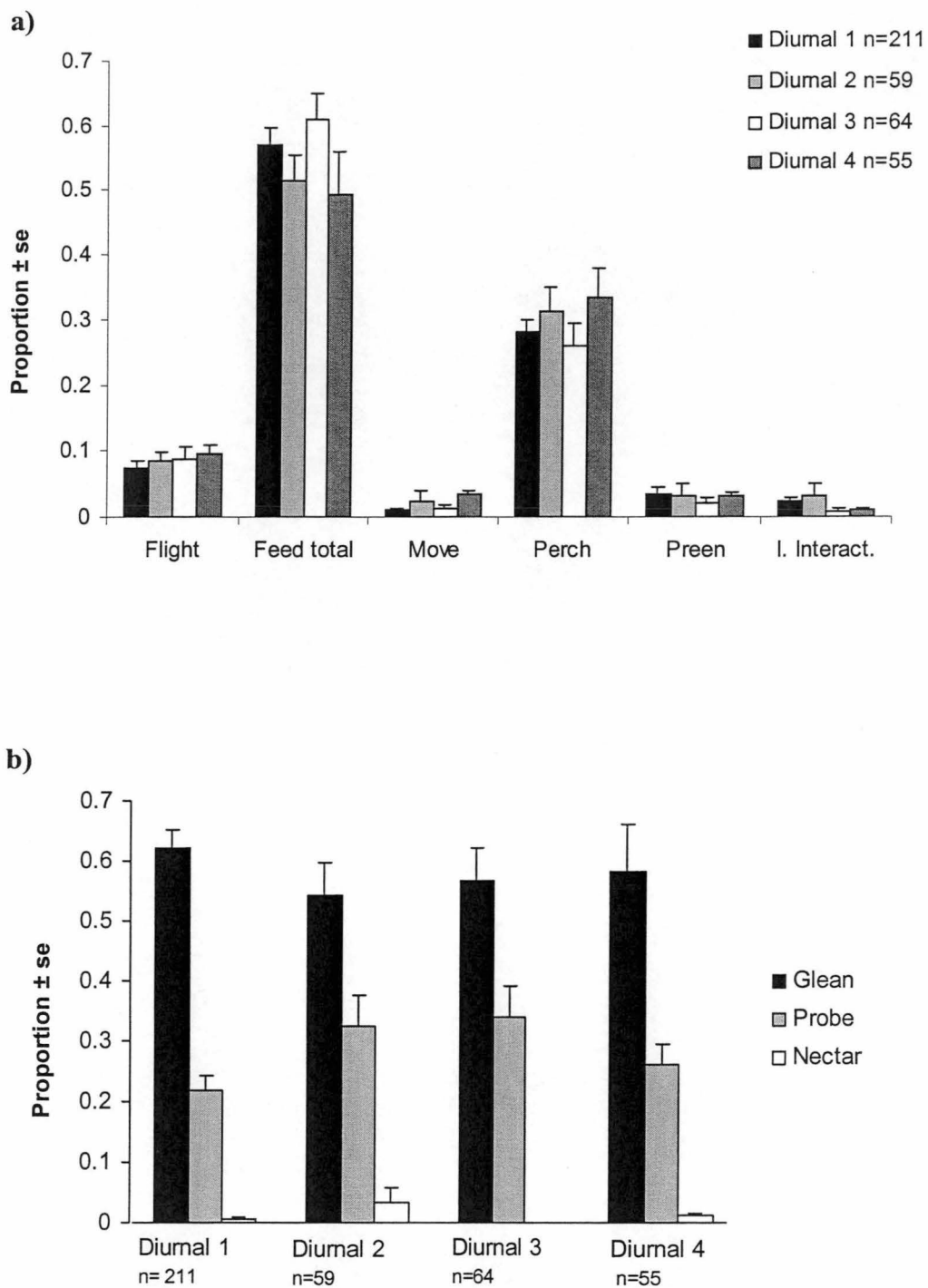


Figure 4.5 a) Average proportion of time allocated to behaviours over diurnal periods b) Average proportion of time allocated to foraging method over diurnal periods. Diurnal periods one being early morning to mid morning (sun angle $45^\circ < \text{angle} < 90^\circ$), two mid morning to midday (sun angle $0^\circ < \text{angle} < 45^\circ$), three midday to mid afternoon ($315^\circ < \text{angle} < 360^\circ$) and four being mid afternoon/sunset (sun angle $< 315^\circ$).

Table 4.2 Tukey post hoc analyses showing where significant diurnal variations occur in behaviours ($\alpha=0.008$).

| | Forage (total) | | | Move | | | Interactions | | |
|----------------|----------------|------|---|-------|-------|-------|--------------|---|------|
| Diurnal Period | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| 1 | | | | | | | | | .001 |
| 2 | | | | | | | | | |
| 3 | .006 | | | | | | | | |
| 4 | .002 | .006 | | >.001 | >.001 | >.001 | | | |

Foraging behaviours also appear to be influenced by diurnal periods. Figure 4.5b shows that the time spent gleaning is greatest in the morning. It plateaus out across the rest of the day. Probe shows a reverse trend, with an increase in this feeding method in the middle of the day. Significant differences were calculated for both feeding methods; glean ($\chi^2 = 22.883$, d.f. = 3, $p < 0.001$), probe ($\chi^2 = 25.670$, d.f. = 3, $p < 0.001$). Diurnal period 2 was found to significantly differ from all other periods for both glean and probe respectively – 1 ($Z = -4.330$, $P < 0.001$; $Z = -4.722$, $p < 0.001$), 3 ($Z = -3.802$, $p < 0.001$; $Z = -3.807$, $p < 0.001$), 4 ($Z = -4.040$, $p < 0.001$; $Z = -4.040$, $p < 0.001$) (Bonferroni adjusted $\alpha = 0.008$). Seasonal implications on diurnal behaviours were not considered as sample sizes were considered too low to make meaningful comparisons.

The results obtained for this study suggest that for *M. affinis*, time budget does not change between breeding and non-breeding seasons. Annual changes in environment influence the time allocated to different behavioural groups. Season significantly affects the foraging method, though time allocations to other behavioural groups are constant. However, diurnal period, or more accurately sun position, does influence the behaviour of *M. affinis*.

Foraging behaviour was found to significantly vary between breeding and non-breeding period, season and diurnal grouping.

4.4 Discussion

How a species adapts to its environment is vital to its long term survival. Being an endemic species, it would be assumed that *M. affinis* has adapted to specific conditions of the Tasmanian environment. The two major variations (when compared to the mainland of Australia) as defined by Ridpath and Moreau (1966) that strongly influence the avifauna of Tasmania are climatic variations and the availability of appropriate food resources. Lower mean temperature and lower summer temperatures in Tasmania compared to the mainland substantially impact upon food resources (Ridpath & Moreau 1966). Though rainfall is evenly distributed across the year, the increase in summer temperatures can reduce the effectiveness of precipitation, drying out the land and vegetation. This tendency strongly affects vegetation, and subsequently influences the reproduction and mortality of animals (Ridpath & Moreau 1966). During the period of this study the rainfall encountered across all study sites was well below average for the first breeding/non-breeding cycle, and then above average for the second breeding cycle. It is suggested that this limit in water availability was an important factor behind the variations encountered in the behaviour of *M. affinis* over the duration of this study.

Rainfall influences the abundance of arthropods present in both canopy and understorey vegetation (Bell 1985a; Frith & Frith 1985; Abbott *et al.* 1992; Recher *et al.* 1996). No such data is available for the study region; however, variation in rainfall and temperature over successive summers and years possibly influenced the abundance of eucalypt-feeding chrysomelid (Greaves 1966 cited in Abbott *et al.* 1992), and McQuillan *et al.* (1998) suggest that hot, dry summers can impact upon the abundance of Lepidoptera in Tasmania.

If this trend is consistent for Tasmania it could be suggested that this is strongly influencing the behavioural variations observed through out this study.

The general concept being suggested by all results is that within a year the behaviour of *M. affinis* varies little between either season or between breeding and non breeding periods. This lack of seasonal variation in *M. affinis* may

be accounted for in a number of ways. Firstly, season might not influence the behaviour of *M. affinis*. This could logically be argued if rainfall (or water availability) was the driving force behind this species responses, and as seen by data obtained from the Bureau of Meteorology, the rainfall in Tasmania is fairly consistent across all seasons. Hau's (2001) research indicates that birds may respond to rainfall cues directly. Thus consistent rainfall across Tasmania in all seasons would invoke a consistent behavioural response in *M. affinis*. Low seasonality in the Tasmanian climate may contribute in dampened seasonal changes in behaviour.

Secondly, the lack of variation between breeding and non-breeding behaviours could be due to observation being incidental, ie there was no selection for specific individuals and monitoring of their behaviour during breeding and non-breeding season. Thus there is the possibility that the majority of observations during the breeding period are of non-breeding birds, and so behavioural changes were not observed. Though this possibility should be considered, it is not likely, as focal birds were followed back to nest sites on numerous occasions, and obvious breeding behaviours (such as bonding displays and courtship feeding) were recorded for some individuals.

When considering annual variation in behaviour, significant change is apparent. The proportion of time allocated to behaviours varies significantly between years, though between breeding and non-breeding of the same year, behaviour varies little. Drought conditions and subsequent impact on resource availability is suggested to cause these variations in behaviour. Oliver (2001) suggested that drought strongly influenced behavioural changes in *Xanthomyza phyrigia*, Regent Honeyeater, between years, as reduced water availability suppressed the flowering of *Eucalyptus* sp. thus nectar availability, causing birds to switch resource type to satisfy their energy demands.

Between the four breeding and non-breeding seasons, substantial changes in foraging are seen. The second period (non-breeding 2001), most strongly influenced by restrictions in rainfall, shows significant increase in the amount of time *M. affinis* allocated to probing behaviour, thus utilizing a different

resource base during periods of environmental hardship. With the increase in rainfall, feeding behaviour is seen to shift back to foliage gleaning, a feeding method consistent with the available literature on this species. Both Thomas (1980) and Slater (1994) recorded foliage gleaning as the foremost feeding method for *M. affinis*, consistent with classifying this species as a foliage specialist (Keast 1968a, Thomas 1980). Cale (1994) however, regards *M. affinis* as a nectarivorous species in his study, based on the observation that these birds fed only within the blossom of *Eucalyptus sp.* This assumption discounts the possibility that during this period of time insects were being taken from the flowers as well as nectar (McFarland, 1984).

Evidence from Thomas (1980), Slater (1994) and the current study indicate that nectar is not a major carbohydrate source for *M. affinis*. Morphological adaptations support the notion that other carbohydrate sources (such as lerp, honeydew and manna) are of greater importance to *M. affinis* than nectar. Cranial osteology also suggests that alternate carbohydrate sources and insects play a more important role in the diet of Melithreptids, with the evolution of ectethmoid-mandibular articulation in this genus (Bock & Morioka 1971). This mandibular articulation is coupled with a mucus duct behind the upper jaw. This allows the tongue to be protruded through a slight gap between the jaws, moving against the mucus duct, coating the tongue in a sticky mucus. Bock and Morioka (1971) conclude that members of the Melithreptus genus capture insects with this sticky tongue.

Keast (1968a) describes the Black-headed Honeyeater as being more “warbler-like” than other members of the genus, in its shorter bill and hallux. Thus, morphological features are similar to those of a specialized foliage gleaner (eg *Pardalotus*, *Acanthiza*) than the more generalized ones apparent in other Melithreptids (Keast 1968a). Green (1995) found protein supplements were necessary if body condition in captive birds as was to be maintained, providing further evidence of the importance of a protein source such as insects (McFarland 1984) in the diet of *M. affinis*.

Though morphologically adapted to foliage gleaning, as other insular organisms, *M. affinis* has the ability to shift “niche” when necessary. This is

seen with the significant increase in the time spent foraging on trunk and bark (probing) when conditions were harshest, and presumably other food resources were at their lowest. During this time period, birds were also noted to be taking fruit from *Exocarpus cupressoides* as well as probing into insect galls on *Acacia dealbata*.

Seasonally, similar changes are observed with changes in resource availability and predominant feeding method. Bell (1985a) showed patterns of summer peaks and winter lows in biomass of arthropods, findings similar to many other studies (e.g. Frith & Frith 1985; Abbott *et al.* 1992). Noske (1983a cited in Bell 1985a) showed that during winter, arthropod numbers found within the bark of Eucalypts peaked. If similar trends are seen in Tasmanian arthropods, this may explain the significant change in feeding method from feeding in the canopy to feeding on trunk and within bark, by *M. affinis* with seasons. This is consistent with findings by Carpenter (1978) who hypothesised that honeyeaters were not limited by nectar resources, but perhaps by insects.

Oliver (2000) points out the scarcity of literature considering variations in foraging behaviour from year to year in avifauna. He noted that those few papers available do not provide any quantitative evidence on resource abundance. This is also true in this study, however the yearly shifts in behaviour are evident. It is likely however, that there is a relationship between season, arthropod abundance and foraging behaviour, as well as influence by drought conditions.

4.4.1 Diurnal Variations

There is no conclusive evidence the diurnal periods significantly influence avian behaviour. Various studies have found differing evidence as to the importance of daytime on birds. For example, Paton (1982) found little variation in foraging activities in the New Holland honeyeater (*Phylidonyris novaehollandiae*), except in the summer, when activity decreased during the middle of the day when temperatures were increased. Runciman (1996) also found the frequency of behaviours in non-breeding Helmeted Honeyeaters, *Lichenostomus melanops cassidix* did not change significantly between morning (before 1300) and afternoon (after 1300). Other studies have

recorded behavioural changes between diurnal periods. Collins and Briffa (1983) proposed in broad terms that the Brown Honeyeater, *Lichmera indistincta* has an increased activity level in the morning compared to the afternoon. This is thought to reflect nectar availability, with standing crop being higher in the morning.

Oliver (2001) found that for Regent Honeyeaters, *X. phrygia*, time of day may influence behaviour. Morning (defined as the first three hours after sunrise) found birds to generally increase activities, such as foraging, with more time spent resting during the middle of the day. When data across all study sites was pooled, foraging and resting behaviours were consistent across the day, but aggressive behaviours were significantly increased in the morning.

Current data suggests differences occur between the morning and afternoon in time budget for *M. affinis*. Collins and Briffa (1983) and Runciman (1996) both associate diurnal variation (or lack of) in behaviour to be associated with the availability of food resources through out the day. This may be a driving force behind the changes observed in foraging behaviour for *M. affinis*. Oliver (2000) relates diurnal changes in the nectar availability to diurnal changes in feeding behaviour of *X. phrygia*. There is some evidence to suggest that nectar availability fluctuates throughout the day. Ford (1979) stated that nectar availability peaked in the morning. This perhaps explains diurnal variation in behaviours for some species of honeyeater, as Yuni (2002) suggested for *Phylidonyris novaehollandae* in Tasmania. However, with results in this paper showing negligent nectar use for *M. affinis*, this is not a likely explanation for diurnal change in behaviour.

What may be dictating this diurnal change in behaviour in *M. affinis* is sunlight (and subsequently temperature) and the activity of insects.

Early morning activity is necessary for organisms to replenish energy lost over night, leading to an increase in foraging activity. This is seen to occur in *M. affinis*. The activity (and thus detect ability) of the species reduced around 10am and was consistently noted to do so during field observations. This level of activity was low until approximately 1:30pm, consistent with the observations of Oliver (2001) of increased resting during the middle of the

day. Foraging then increased during the early afternoon when temperature and sunlight were higher. One explanation why activity may drop off in the late afternoon at sites RW and RR is temperature decrease. Both these sites are situated at the foot of Mt Wellington. This causes quite a dramatic temperature reduction at these sites as the sun sets behind the mountain. If this temperature decrease is affecting the activity of insects at these sites, it would follow that the foraging of *M. affinis* would decrease as well. This is consistent with the changes in specific foraging behaviours (fig. 5.5b) that shows a decrease in probing in the later afternoon.

Similar temperature and light decreases were noted at site MR. In this instance however, rather than impact across the whole site, there was a gradual change due to the topography of the area. The main sampling area at this site was along the creek line, which is enclosed by steep slopes on both sides. As the sun set, the available sunlight progressed further up the western facing slope and ridgeline, with notable changes in the activity of all bird species in the area. Avian activity continued in areas getting the late afternoon sunlight. These areas are hard to access, so sampling was limited to the lower slope and creek line. This may have resulted in a bias in the data with those individuals settling down to roost being recorded more than those still active.

What should be considered is the way in which data was divided into diurnal period for this study. As it was accomplished using azimuth measurements, it is the position of the sun that is influencing the behaviours observed. The position of the sun may vary the intensity of the light available to foraging birds, or the ambient temperature, both of which would be expected to rouse insects, prompting behavioural responses in birds (Hau 2001; Astheimer & Buttemer 2002).

4.5 Conclusion

This study, whilst aiming to construct simple breeding and non-breeding time budgets for *M. affinis*, resulted in displaying how environmental factors can influence behaviour and how the study species has the ability to adapt to these varying conditions. The data presented for *M. affinis* in this paper suggests that this species did not respond to seasonal indicators with regards to its

time budget. This may be an adaptation to the temperate, maritime type climate experienced in Tasmania, where seasonal fluctuations in rainfall and temperature are not as extreme as elsewhere in Australia (Williams 1974). What the species is potentially responding to is the availability of necessary food resources (as seen with the changes in foraging behaviour), which are influenced by climatic variations.

5. MICROHABITAT AND TREE SPECIES UTILIZATION

5.1 Introduction.

The previous chapter explored the time allocated to particular behaviours in *M. affinis*. This chapter considers the habitat use of the study species at a microhabitat scale.

Though described by Keast (1968a) as more warbler like (family Acanthizidae) in morphology than other members of the family, no studies have been undertaken on the actual habitat preference of *M. affinis*, and, if indeed, it does fill this niche in the Tasmanian environment. There are five representatives of the family Acanthizidae present in Tasmania. These represent three genera: *Acanthiza* with three species, *Sericornis* with one species and *Acanthornis* with one representative. There are no representatives of the genus *Gerygone* found in Tasmania. These species generally remain in the lower canopy of woodlands, or are confined to the undergrowth. The Brown thornbill (*Acanthiza pusilla*) has shown some release, and it is seen to utilize the canopy more than mainland counterparts (Keast 1970). In comparison, the family Acanthizidae has 14 representatives in the south of Victoria, seven of which utilise middle and upper canopy habitats. Also using this habitat are the Pardalotes, three of which are found in Tasmania (compared to two on mainland Victoria). Subsequently the niche of upper and mid canopy foliage, filled by up to nine bird species on the mainland, is relatively free in Tasmania and would allow a niche shift in some species of birds.

The aim of this chapter is to explore the microhabitat use by *M. affinis* to determine if it fills the role allotted to warblers on the mainland, and also determine if specific tree species are selected for.

5.2 Methodology and site description

The methodology used to collect appropriate data for this study and site descriptions have been described in depth in chapter 3. Of note however, is the point that all sites were originally selected due to similarities in the vegetation present. This was done limit the variance in vegetation with regards to the time budget compilation. All sites are dominated by *Eucalyptus pulchella* – *E. viminalis* woodland, with *E. obliqua* present in areas of higher moisture (North 1997;2000). The understorey at each site is open, dominated by grasses and low growing shrubs.

For each site five random plots were determined. These were ten metres in radius. Within each plot the number of each eucalypt species was countered to provide a measure of the proportion of each species in the canopy. As this vegetation community is quite uniform, five plots was deemed representative of the canopy dominance.

Division of data into breeding and non-breeding periods follow that presented in chapters 2 and 4, and the same method of allocating diurnal period were used.

To allocate microhabitat variables the tree in which individuals were observed was recorded. Each tree was divided into thirds, with the estimated top third being allocated the variable of upper canopy, the middle third mid canopy and the lower third of the tree the lower canopy. Undergrowth and ground microhabitat variables were also applied. A total amount of time spent in each microhabitat variable was then calculated.

5.2.1 Statistical analysis.

As data collected was proportional it was first transformed using an Arcsin transformation (Zarr 1999). The Freeman & Tukey (1950 cited in Zarr 1999) transformation was applied (equation 1).

$$p' = \frac{1}{2} [\arcsin\sqrt{X/n+1} + \arcsin\sqrt{X+1/n+1}] \text{ (equation 1)}$$

This transformation was used as much of the data was at extreme ends of

the range (ie near 0 or 100%), and the above transformation results in the widest spread (Zarr 1999).

Transformed data was then tested for both univariate and multivariate normality and collinearity, and found to violate the necessary assumptions to use either ANOVA or MANOVA methods of analysis. Subsequently, non-parametric methods of analyses have been applied.

Tree species utilization was analysed using Kruskal Wallis (Nonparametric ANOVA) as were tree species comparisons between breeding and non-breeding season. Only four species, *Eucalyptus viminalis*, *E. pulchella*, *E. obliqua* and *E. rubida* were tested for seasonal variations, as other species were deemed too infrequent in use to warrant statistical analysis.

Microhabitat use was again found to violate the necessary assumptions for parametric statistical analysis. Kruskal-wallis nonparametric ANOVA and Mann-Whitney U tests were utilised to determine significant variation in time allocated to microhabitat.

All statistical procedures were undertaken using SPSS 10.0 computer software.

5.3 Results

5.3.1 Dominant Eucalypt Species.

Table 5.1 provides the results of the canopy sampling. In combining this data across sites, the ratio of *E. viminalis*: *E. pulchella*: *E. obliqua*: other results as a 1:1.6:1:0.2. This shows that there is almost double the number of *E. pulchella* in this vegetation community to *E. viminalis*. On a site-to-site basis, site MR is the only site where *E. viminalis* outnumbered *E. pulchella*. *Eucalyptus obliqua* is found to be the dominant eucalypt at this site.

5.3.2 Tree Species Utilization

Seven species of tree were used by *M. affinis* during this study. These were *Eucalyptus viminalis*, *E. pulchella*, *E. obliqua*, *E. globulus*, *E. rubida*, *E. risdonii* and *Acacia dealbata*. The distribution of time spent in each tree type can be observed in figure 5.1.

Table 5.1 shows the average number of each canopy species within a 10m radius across each site. *is a combination of *E. globulus* (at sites RW and RR) and *E. rubida* (site MR).

| Site | <i>E. viminalis</i> | <i>E. puchella</i> | <i>E. obliqua</i> | Other* |
|------|---------------------|--------------------|-------------------|--------|
| RW | 3.8 | 8.2 | 3.8 | 0.2 |
| RR | 2.8 | 6.6 | 1.2 | 1 |
| MD | 2.7 | 3.7 | | |
| MR | 4 | 2.6 | 5 | 0 |

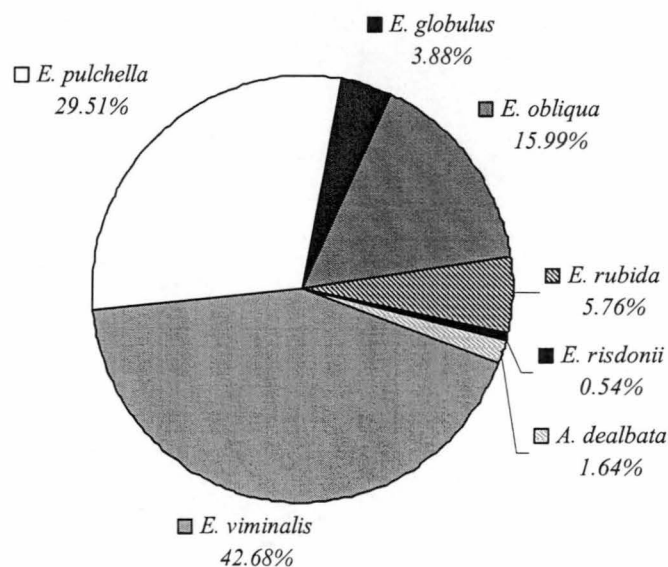
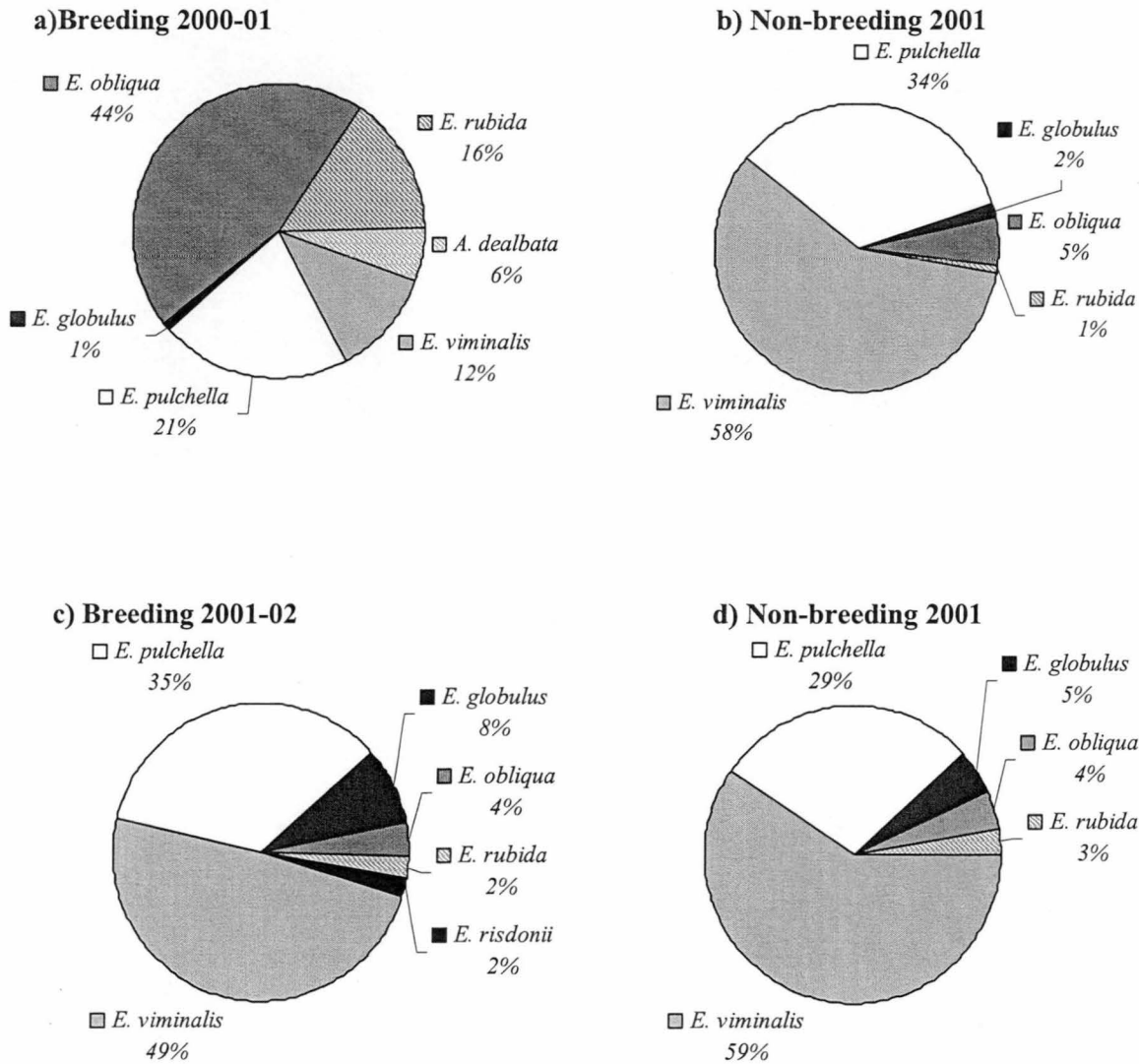


Figure 5.1 The percent time spent in each tree type by *M. affinis*

Pooled data shows that the majority of time was spent in *E. viminalis*, with this being significant ($\chi^2 = 52.060$, d.f.= 4, $p < 0.001$). Comparisons were made between breeding and non-breeding periods, when field site were under the impact of drought and non-drought conditions. The changes in time allocated to each vegetation type can be seen in figures 5.2a – d

Of note is the variation in the number of tree species utilized in figure 5.2a which represents the first and most drought affected period. The time

allocation of the species is distributed over six different species of tree, with the proportions differing from those of the other three periods. During this period, *E. obliqua* is the dominant eucalypt species being utilised with *E. pulchella* and *E. rubida* being secondary.



Figures 5.2a-d show pooled data variation in the time allocated to different tree species across four time periods. a) breeding 2000-01, b) non-breeding 2001, c) breeding 2001-02 and d) non-breeding 2002

The time spent in *E. viminalis* is reduced and *Acacia dealbata* is also being used. The other three periods more closely reflect the total proportions of tree utilization seen in figure 5.1. Across these four periods, *E. viminalis*

is found to vary significantly ($\chi^2 = 18.504$, d.f. = 3, $p < 0.001$) as do *E. obliqua* ($\chi^2 = 9.012$, d.f.=3, $p = 0.029$) and *E. rubida* ($\chi^2 = 11.673$, d.f.=3, $p = 0.009$). *Eucalyptus pulchella* was used consistently across all time periods. These are the results obtained when data is pooled across all sites. However, if site MR is removed from the analysis (this site has a permanent water supply) there is no significant variation in the tree species selected for utilization between drought and non-drought periods.

5.3.3 Microhabitat

Microhabitat was divided into upper mid and lower canopy use, with records of undergrowth or ground use also taken. The latter three habitats were rarely encountered, and thus not involved in analysis. *M. affinis* was found to spend significantly more time in the upper canopy than the mid canopy ($Z = -3.011$, $p = 0.003$). Figure 5.3 shows the separation of microhabitat with tree species. *E. viminalis* makes up the greatest proportion for each of the microhabitats. *E. pulchella* is reduced in the lower canopy, with *E. globulus* increasing.

Microhabitat was explored using the same time periods applied in the time budget analysis (chapter 5): season, total breeding and non-breeding, individual breeding and non-breeding seasons and diurnal periods (figures 5.4 a-c). The only time period to show significant variation in microhabitat use was that of diurnal, with significant variation in the time spent in the upper canopy ($\chi^2 = 14.922$, d.f.=3, $p = 0.002$), which shows an increase in the afternoon. Microhabitat was not found to vary with tree species being used.

The foraging substrate being used by *M. affinis* was analysed, as this is the characteristic most strongly influential on the morphology and role played by the study species in Tasmania. Foliage utilization made up 63.2% of total foraging time, trunk/branch utilization 33.0% and blossom usage 3.8%.

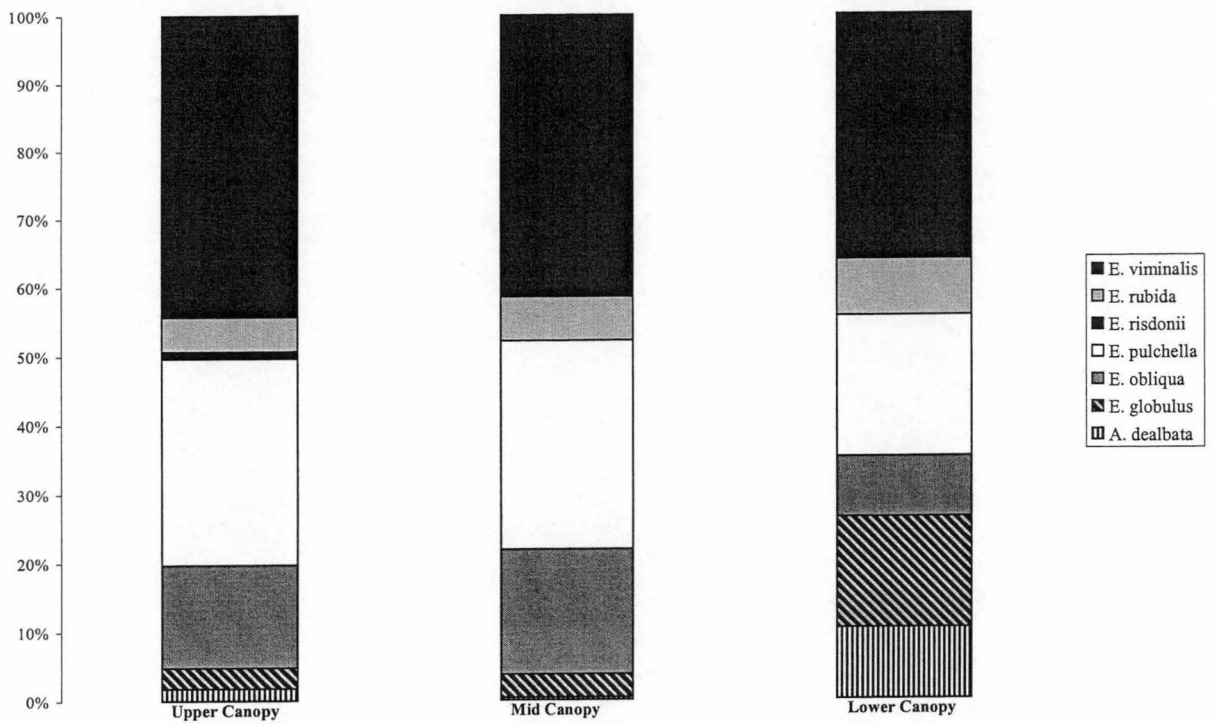
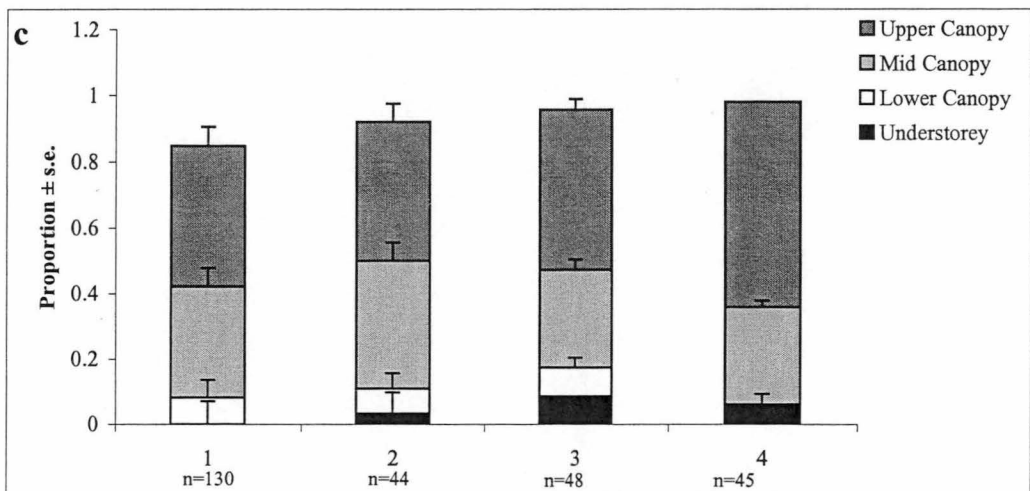
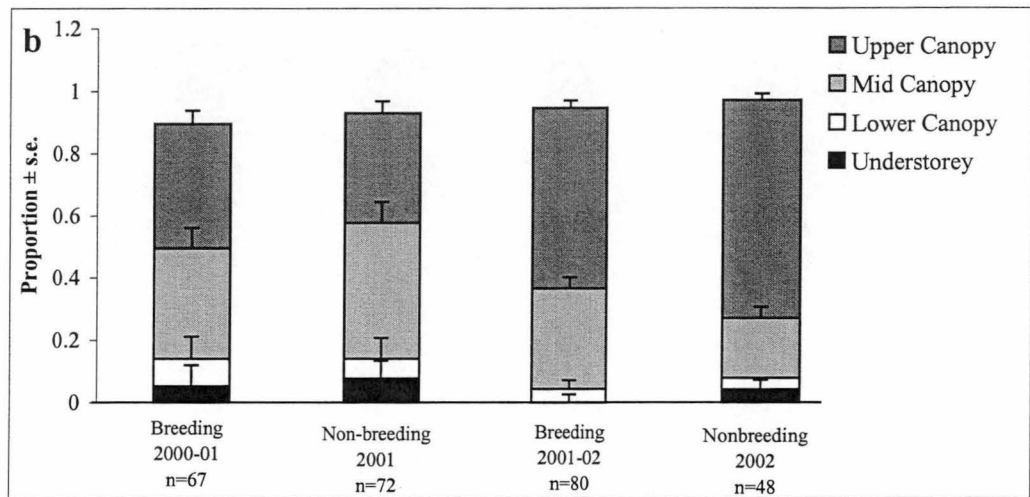
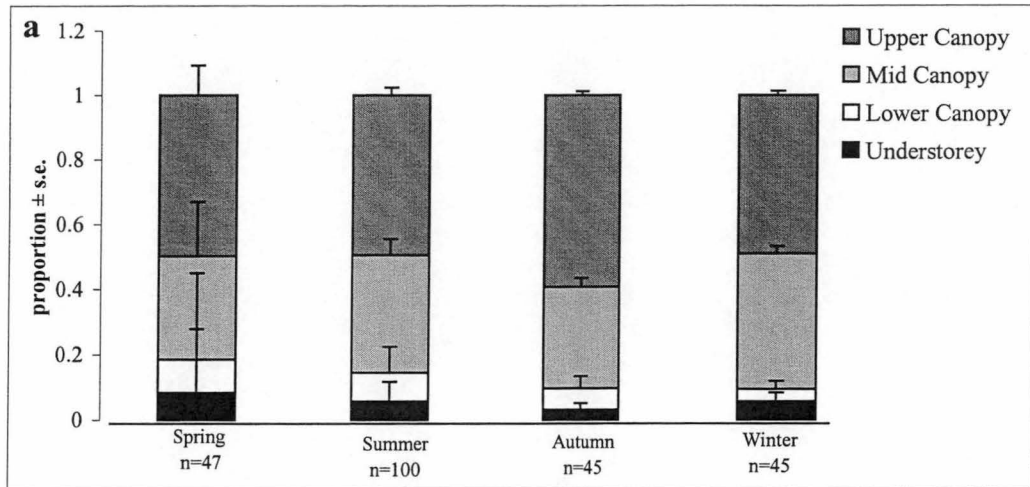


Figure 5.3 The percent of time spent in each microhabitat that was spent in each tree species.



Figures 5.4a-c Show the changes in microhabitat (\pm s.e.) with a) season, b) breeding (BR) and non-breeding (NBR) periods and c) diurnal variation. Diurnal groups follow that defined in chapters 3 and 5, using the azimuth to divide into diurnal groups. Diurnal period 1 is early morning, 2 mid morning to midday, 3 midday to mid afternoon and 4 mid afternoon to sunset.

5.4 Discussion

The habitat use by *M. affinis* across the study sites is one of upper canopy and foliage dominance. The species forages in a variety of *Eucalyptus* species, with significantly more time apportioned to *E. viminalis* (White gum)¹ than other species during times of ‘normal’ conditions.

The results presented above suggest an association between *M. affinis* and *E. viminalis* at the current study sites, even though this eucalypt species is not the dominant canopy species across this woodland type (North 1997; 2000). Woinarski & Bulman (1985) state that for this species of eucalypt, the abundance of manna produced (manna is the sugary fluid that exudes from damaged plant material Paton 1980) is substantially greater than in other eucalypt species; with the possible exception of the closely related *E. dalrympleana* (Mountain White Gum – also found in Tasmania). Observations of *M. affinis* collecting manna and the presence of lerp were recorded during the study period.

This association with *E. viminalis* is known in other Tasmanian birds, particularly within the endemic component. The Forty-spotted Pardalote (*Pardalotus quadragintus*) is associated with the presence of *E. viminalis*, to the point that it almost exclusively utilises this one species of tree (Woinarski & Bulman 1985). Strong competition occurs between *M. affinis* and *P. quadragintus* for resources within *E. viminalis* woodland (Woinarski & Bulman 1985). This suggests the importance of this tree species to aspects of the Tasmanian avifauna.

However, *M. affinis* is not restricted to this vegetation type in the way that *P. quadragintus* is. Recher *et al.* (1971) found that *M. affinis* was most abundant in *E. dalrympleana* woodland. Personal observations at Lake St Clair (42° 07', 146° 10') also found high numbers of *M. affinis* in *E. dalrympleana* woodland. Unfortunately, HANZAB (2001) makes no reference to *E. viminalis* with regards to *M. affinis*, potentially excluding a vital vegetation type utilised by the study species.

¹ Common names as of Page (1998)

The importance of *E. viminalis* and its provision of an alternate carbohydrate source is further emphasised when one considers the small amount of time *M. affinis* is observed in the blossoms. The previous chapter also suggests that for the period of the study that nectar use was negligible in the diet of the study species. Paton (1980) states that Manna (plus two other carbohydrate sources – honeydew and lerp) is an important substitute for nectar. His study found a high availability of manna within *E. viminalis*, with this alternate carbohydrate source more abundant than insects and other arthropods across most substrates utilized by birds. The energy rewards of manna were also calculated as being substantially greater than those of insects. Paton's (1980) study found this resource to be important in the diets of *M. lunatus* (White-naped honeyeater), *M. brevirostris* (Brown-headed Honeyeaters) and *M. gularis* (Black-chinned Honeyeater). There was a strong seasonal component to this resource utilization, with traditional carbohydrate sources (nectar) being used in the early spring, when available. Conversely, records of *M. affinis* in the blossoms of eucalypts were negligible during this study. This may be due to the limited (if any) flowering of eucalypts across the study period. However, other studies have shown this species to have very limited nectar use. Thomas (1980) had no record of nectar use, and Slater (1994) also found *M. affinis* to rarely utilize nectar resources. Thus, this species is probably accessing alternate carbohydrates, such as manna, which suggest an important relationship between the white gums (*E. viminalis* and *E. dalrympleana*), and *M. affinis*.

A wide variety of plant types are exploited by *M. affinis* during periods of environmental pressure. The obvious change is in the species of tree being used during periods of increased dryness. During the most drought impacted period, *E. obliqua* (Brown-top Stringybark) was seen to be utilized more so than other species. This species of eucalypt shows a preference for areas of greater moisture content (in the case of site MR these were most abundant along the creekline) (North 1998; 2000). Thus for this tree species, the moisture reduction may not have been as severe during the drought than for other species, allowing a continued insect abundance upon which the study species could feed. The spatial distribution of *M. affinis* was observed to

differ during the harsher drought periods, with more birds being consistently located along creeklines and drainage lines, or in the case of site RR along the edge of the reservoir, where *E. obliqua* is more frequently found. This trend was anecdotally noted for other woodland birds during the drought period. The rough bark of *E. obliqua* may provide shelter for insects during the periods of dryness, further contributing to a greater insect abundance upon which the study species could feed. Thus a combination of moister habitat and shelter for arthropods may explain why *E. obliqua* was used significantly more during the first breeding period, and subsequently limited in use thereafter.

Two other tree species show interesting usage. The first of these is *Acacia dealbata*. This was only used during the drought period. Birds were observed taking larvae from wasp galls along the branches of the plant. Again, this is probably not a primary food source for *M. affinis*, but exploited during times of environmental stress.

The second tree that shows interesting trends is that of *E. pulchella* (Narrow leaved Peppermint). The use of this species does not change at all during the study period. What this suggests is that *E. pulchella* (though the dominant eucalypt species at most sites) provides a consistent, though secondary resource, for *M. affinis* all year round, no matter the conditions.

The choice of White Gum and Peppermint habitat by *M. affinis* is consistent with the small amount of literature available on this aspect of the species' ecology. Recher *et al.* (1971) found the highest abundance of *M. affinis* in *E. dalrympleana* woodland, with records of the species nesting in this woodland type. Thomas (1980) found *M. affinis* in woodland dominated by *E. globulus* (Blue Gum), *E. amygdalina* (Black Peppermint) and *E. linearis* (White peppermint). LeFort (2002) found the greatest abundance of *M. affinis* within *E. viminalis*, *E. pulchella* and *E. amygdalina* (Black Peppermint) woodland, further indicating this species preference for White Gum and Peppermint woodland.

The morphological features of *M. affinis* have been described elsewhere (Keast 1968a; Bock & Morioka 1971). This chapter provides evidence as

to how these features relate to habitat use. There is no disputing that *M. affinis* is a canopy specialist, foraging predominately amongst the foliage. Keast (1970) suggests that *M. affinis* fills an unoccupied niche, left vacant in Tasmania by the lack of warblers.

The family Acanthizidae contains many of Australia's small insectivorous species of bird, such as *Sericornis*, *Acanthiza*, and *Gerygone* (Keast & Recher 1997). Each of these genera is small bodied, an insect specialists, and fills a specific niche, with a limited amount of overlap. Of these genera *Sericornis* and *Acanthiza* are represented in Tasmania. *Sericornis* are the undergrowth dwelling scrubwrens. *Acanthiza* are the thornbills, with no representatives in Tasmania considered to be upper canopy specialists. The two Tasmanian species are *Acanthiza pusilla* (Brown thornbill) and the endemic *A. ewingii* (Tasmanian Thornbill). In mainland habitats *A. pusilla* forages mainly in the understorey, probing into densely-packed foliage (Bell 1985b), with the upper canopy foliage utilized by *A. lineata* (Striated Thornbills) and *A. nana* (Yellow thornbills). Tasmania sees a shift in the habitat use by *A. pusilla* to use the upper foliage of eucalypt species, a niche that it does not generally use on the mainland (Keast 1970).

The third genus, *Gerygone* is the genus that encompasses the Australo-Papuan warblers. This genus is not represented in Tasmania. In a study on adaptive zones of this genus, Keast and Recher (1997) established that aerial foliage is significantly made use of, with any observations of trunk/branch use also being within the upper third of the tree – a niche very close to that observed in *M. affinis*. Conversely to *M. affinis* however, *Gerygone* are wholly insectivorous (Keast & Recher 1997), suggesting that whilst foraging substrate overlaps, there may be a difference in the resources utilized.

Habitat use by *M. affinis* in Tasmania is more similar with that of the Pardalotes (family Pardalotidae). These are small leaf gleaning birds, the major component of their diet being lerps (Woinarski 1985b). There is known competition between these species of birds and *M. affinis*, with *M. affinis* being the more aggressive species (Woinarski & Bulman 1985).

5.5 Conclusion

M. affinis is a canopy, predominately foliage specialist, that utilises the same niche year round. In times of environmental pressure the species is able to change the tree species upon which it forages but does not substantially change the section of the tree being utilized.

There is a preference in *M. affinis* tree selection for *E. viminalis*, a species of eucalypt known to possess a high level of manna, a characteristic that already explains the strong association of some other avian species (Woinarski & Bulman 1985). Further research is necessary into the actual items upon which *M. affinis* forages to determine the level of manna and lerp in the species diet. *E. pulchella* provides a resource that is consistently utilized, though is never the dominant eucalypt chosen, suggesting it to be important as a secondary resource.

Whilst *M. affinis* shows a strong preference for habitat and foraging substrates similar to those in the *Gerygone* sp. on the mainland, potentially, different resources are being utilised by the Tasmania species. *Gerygone* are totally insectivorous (Keast & Recher 1997), but there is evidence to suggest that *M. affinis* accesses alternate carbohydrate sources found within the foliage on eucalypts as well as taking insects, making it similar in foraging to the pardalotes (Woinarski & Bulman 1985).

6. BREEDING BIOLOGY OF *MELITHREPTUS AFFINIS*

6.1 Introduction

The honeyeater family (Meliphagidae) is one of the most diverse avian families found within Australia. Despite this, limited research has been undertaken with regards to the breeding biology of most members of this family. Those species which have been studied are either of conservation value, for example *Xanthomyza phyrigia* (Geering & French 1998; Oliver 1998) and *Lichenostomus melanops cassidix* (Franklin *et al.* 1995), large and conspicuous; *Anthochaera carunculata* and *Philamon corniculatus* (Ford 1999) or strongly sedentary and colonial such as *Manorina melanocephala* (Dow 1978) and *M. melanophrys* (Clarke 1988; Poiani 1993). These trends are not limited to honeyeaters particularly, but are encountered across the general avian literature published in Australia (Clarke 1997). In this review, Clarke (1997) also found strong biases towards avian species from more temperate climatic areas. Thus, much of the study undertaken on the breeding biology is of “convenient” species.

Some literature is available on the breeding biology of tropical North Australian honeyeaters (Noske 1998), however, at the other extreme, southern, Tasmanian species, there is little literature available.

Limited study has been undertaken on any Tasmania passerine with regards to breeding biology. Fitting with the biases described above, intensive studies have been conducted on the Forty-spotted Pardalote *Pardalotus quadragintus* (Woinarski & Bulman 1985) a species of conservation value, and on the Tasmanian Native Hen (Ridpath 1972), a large, conspicuous co-operative breeder. With regards to honeyeater species, of which Tasmania supports ten including the largest member of the family *Anthochaera paradoxa*, the only scientific study undertaken on breeding has been by Bruce (1988), where two nesting attempts of *L. flavicollis* were described. This is disappointing as the state has a different climate to other areas of the country, and has been exposed to a distinct geological history where it has been attached to and isolated from continental Australia.

The aim of this chapter is to describe and quantify aspects of the breeding

biology of *Melithreptus affinis*, an endemic island avian species, using historical data and a current field based study. All aspects of breeding are considered from the initial bonding of breeding pairs through to fledging of young. These results will then be used to determine if the breeding of this species differs from more temperate mainland honeyeaters or if island effects defined in other situations, are applicable in a Tasmanian context.

It would be expected that the climate of Tasmania would influence aspects of the breeding biology of the species. There is evidence that many Australian mainland birds are flexible breeders (Astheimer & Buttemer, 2002). That is, when environmental conditions are favourable (no matter what time of the year) successful breeding may occur. This is reflected in the relative stability of mainland climates. Conversely, Tasmania tends to have much greater fluctuations in seasonal climate. With only 4.5 good breeding months available in Tasmania (Thomas 1978) it would be hypothesised that the breeding season of *M. affinis* would be finite and shorter than mainland species where the number of good breeding months is doubled.

The island aspect may also exert a substantial influence on the breeding biology of *M. affinis*. Current literature in the Northern Hemisphere (Wiggins *et al.* 1998; Higuchi 1976) suggests substantial shifts in the breeding biology of island populations compared to their mainland counterparts. Island populations tend to have lower clutch sizes (Cody 1966), later laying dates, prolonged nestling development and (in some cases) increased adult survival (Wiggins *et al.* 1998). Other characteristics such as fecundity and nesting success have also been considered, and again in some instances, significant variation has been observed between insular and mainland populations (Blondel *et al.* 1992).

6.2 Site Description

An extensive description of field sites utilised has been given elsewhere (see chapter 2). For the purposes of this study, 6 field sites were regularly surveyed for nesting activity. These were Ridgeway, Ridgeway Reservoir, Meehan Ranges, University Reserve, and Knocklofty. Mount Direction was introduced late in the 2001 - 02 breeding season.

6.3 Methods

A description of the methods employed during this study have been described elsewhere.

Attempts were made to mist net individual birds during the breeding period. Standard mist nets were used. As the species is a canopy species, various methods were employed to try to lure the birds down into the nets. This involved the use of decoy birds – either a paper mache` black-headed honeyeater or a stuffed Pallid Cuckoo (*Cuculus pallidus*) or Shining bronze Cuckoo (*Chrysococcyx lucidus*); and call playback of territorial, contact or juvenile calls of *M. affinis*, or the appropriate cuckoo call. Generally, both methods were employed together.

The response of individual birds varied from no response at all, to a vocal response through to physically searching out the source of the call. Fourteen mist net hours were undertaken, with only one capture. Subsequently, banding attempts were abandoned, as the time commitment necessary did not produce adequate results.

Sexing birds in the field is difficult as there is no sexual dichromatism in the species. There is however, sexual dimorphism, with the male being significantly larger than the female (HANZAB 2001). Data obtained from the ANWC also indicates the presence of a brood patch in female birds whilst breeding. It was possible in some instances to see the developed patch in the female of a breeding pair. It was also possible to determine male and female birds in single pairs due to size differences, so in some instances that gender

of nesting birds was determinable. Difficulty was experienced in cases where extra birds were involved in nesting attempts.

Once nests were located, data was collected on the site selection of the nest (see chapter 2, section 2.4.4 for details). Nests were monitored every one to two days after location. Egg laying and hatching were inferred from adult behaviour (Tremont & Ford 2000) as active nests were over 10m. The use of juvenile vocalization was also used to indicate hatching and the continued activity of nests.

Nests were labelled based on the site, the number of breeding attempts already found and the year. For example, the third breeding attempt at site RW in 2001 was labelled RW301.

To calculate the proportion of young in the population, total number of banding records of juveniles for each breeding season (including first year birds from the following season) were divided by the total number of banded birds in the season.

Historical data from the Queen Victoria Museum and Gallery (QVMG), Australian Museum, Victoria Museum and Australian Natural Wildlife Collection (ANWC) was collated and interpreted in combination with field data.

6.3.1 Statistical analysis.

Nest success was calculated using both raw data and Mayfield's (1975) method of nest analysis. This method compensates for the late discovery of many nesting attempts.

Chi-squared test and non-parametric ANOVA were employed to determine statistically significant differences.

6.4 Results

Three breeding seasons were explored for nesting activities. These have been designated the 2000-01 season, 2001-02 season and 2002-03 season. During these three seasons, 42 nesting records were obtained. These varied from initial building of nest sites, through to the record of fledged young. Of these 42 records, 17 were of actual nesting attempts. Seven complete records of nesting instances were obtained.

Combining field data with historical data, a total of 101 breeding records were obtained. Of these 74 were of nest sites, 29 were nest samples, 44 records of clutches and 54 individual egg measurements.

6.4.1 Breeding phenology.

The first signs of breeding behaviours were observed in late August, when flocks that had formed during non-breeding periods were seen to disperse. This was followed by the occurrence of bonding/mating displays. Bonding displays consisted of male wing fluttering, choralling and pursuit activities, where the male aggressively pursues the female bird. Allopreening is also common in this species, as is courtship feeding. Once pairs have been established physical re-affirmation of the bond is common. Behaviour such as head rubbing is also common. One observation of copulation was taken, with the male mounting the female three times in quick succession. The whole event lasted no more than a few seconds.

Variations in environmental conditions were seen to affect the occurrence of breeding in the species. Limited breeding activities were located during the first breeding period (12 records), and increase in the second (25 records) again decreasing during the third breeding (5 records) period. Few courtship displays or courtship feeding events were recorded for the 2002-03 breeding season. The majority of birds encountered over this period were still in large flocks, suggesting that very few breeding attempts were made over this period; consequently few records were obtained.

The first nesting attempts were found in September for all breeding seasons.

The earliest confirmed nesting attempt was 6th September 2001. One nest is recorded as June. This is an historical record of a clutch collection dated 26/7/1888. Figure 6.1 presents the distribution of nesting attempts per month for 74 nesting attempts (42 records from current study, 32 historic records). It should be noted that for field nesting attempts, the onset of nesting has been inferred for breeding attempts located at fledgling stage.

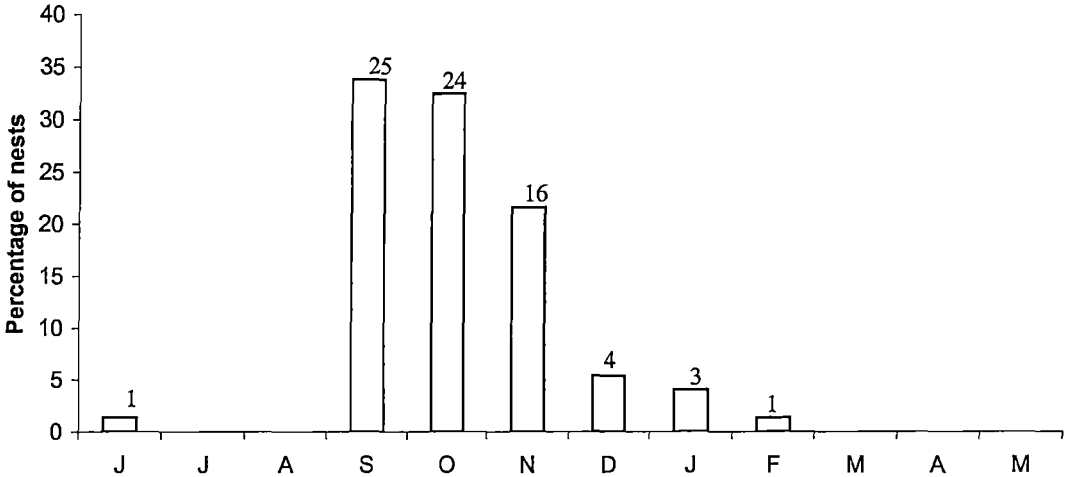


Figure 6.1 Monthly distribution of clutch initiation in *Melithreptus affinis*. Combined data from current field study (n =41) and historical data (n= 34) Total number of records used n=75.

6.4.2 Territoriality and site tenacity.

Once breeding pairs have been established, a nesting territory is established. The breeding pair defends this with strident vocalization when an intruder bird is present. If there is no response to the calls of the territorial pair, intruders are physically chased from the territory. One territory (RW201) was measured during the 2001-02 breeding period, as birds responded to playback calls. Breeding birds would fly to trees on the edge of the territory, and call from these points. The measured territory had a total area of 1088 m², presented as a schematic diagram in figure 6.2. Though this territory is established, feeding occurs both internally and externally to the boundaries. At site MR, many of the birds continued to feed along the creek line, though nest were situated over 100m from the creek itself.

The proximity to a fresh water supply seems to be a common occurrence in the location of this species' nest. Of all records (both historical and otherwise) 16 nests are located in close proximity to creek lines. All RW nests are within 200m of the Ridgeway Reservoir.

There is a strong indication of breeding site tenacity in this species. Over the three breeding seasons, four nests were located around the measured territory. Three of these fell within the established boundaries (RW 500, RW201 and RW102), and the fourth was the original nesting attempt of birds at RW500.

6.4.3 Nest Construction.

A total of 5 hours, 8 minutes and 45 seconds of observations of building activities were collated. All observations were of nests with a pair of breeding birds. All observations show that the female collects material and builds the nest. Though only the female does any of the actual work on the nest construction, the male accompanies her at all times, perching above her as she collects material from the ground, and flying back to the nest site when the female returns. The male was rarely observed to enter the actual construction. Collection of building materials such as bark, grasses and cobwebs was frequently seen. On average, the female birds visited the nest site every 3mins, 15 sec (s.e. ± 25 secs), to work on the construction of the nest. These building episodes lasted on average 49 secs (s.e. ± 5 secs), but could endure up to four minutes. Males would visit the nest every seven minutes (s.e. ± 1 min 16sec), with visits lasting on average 54 secs (s.e. ± 14 secs).

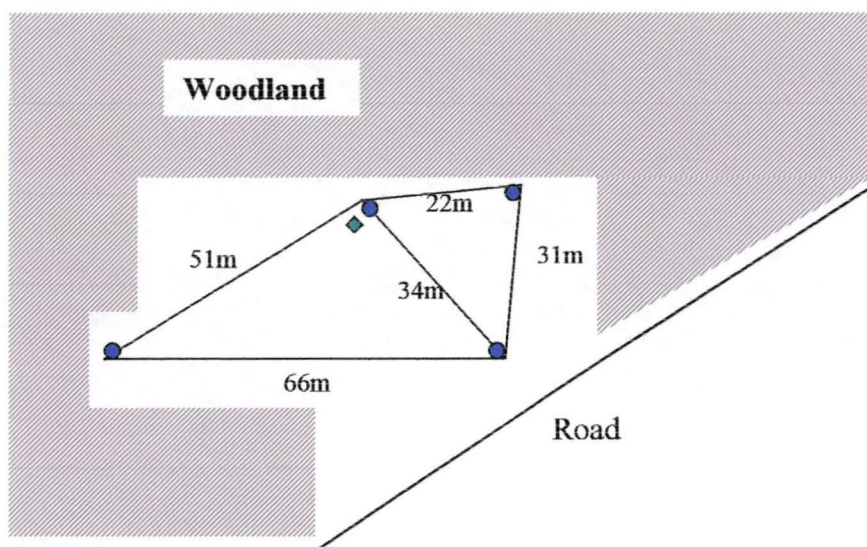


Figure 6.2. Schematic diagram of a nesting territory of *M. affinis*. Drawing is to scale. Blue circle indicates border trees upon which birds would call. Green diamond indicates location of nest within territory.

6.4.4 Nest description.

Twenty nine specimen nests were described and measured by the author.

The nest of *M. affinis* is a deep, cup shaped structure that is suspended from the outer foliage of generally a *Eucalypt* species. These nests are described as pensile nests - that is nest are suspended from a branch by the rim.

Close examination of nest specimens, held by the Queen Victoria Museum and Gallery (QVMAG), Launceston, show one of two methods is employed when suspending nests in the foliage. The first method (shown in plate 6.1 – referred to as supported type) is where the nest rim is built over from 2 to 6 twigs providing support to the structure – figures show the different arrangements of twigs observed. The second method (seen in plate 6.2 referred to as suspended type) is where multiple twigs are attached through the rim, allowing the nest to hang in the surrounding foliage. Up to nine individual support twigs were recorded for this type of structure. Some of the specimen nests showed a combination of the two methods.



Plate 6.1. Nest structure where supports are built into the rim of the nest (supported nest type).



Plate 6.2. Nest structure where twigs are built into the rim causing nest to be suspended in foliage (suspended nest type).

The supported nest type, where twigs are built into the rim of the nest was significantly more frequently utilised by *M. affinis* ($\chi^2 = 7.043$, d. f. = 1, $p = 0.008$) than a suspended nest type.

Nesting materials were found to be predominately sheep's wool (both processed and natural), moss/lichen, cobwebs, eggs sacs of spiders/cocoons, and bark fibres. Nests were lined with wool, feathers, fur (possibly rabbit) or the 'fluff' from the seeds of some plants. As with most constructions, dominant building material depends on what was available to the breeding pair. One nest (plate 6.3) collected from a Stringybark (*Eucalyptus obliqua*), is constructed almost entirely from the bark fibres of the nest tree species, whilst other samples contained little, if any bark fibres.



Plate 6.3: Nest made of Stringybark fibre.

The average size of *M. affinis* nest is presented in table 6.1.

Table 6.1 presents the average size and weight (and standard error) of *M. affinis* nests. For all measurements, 29 nests were sampled, specimens held by QVMAG.

| External Diameter (mm) | Internal Diameter (mm) | Wall thickness (mm) | Total depth (mm) | Internal depth (mm) | Basal depth (mm) | Weight (g) |
|-------------------------------|-------------------------------|----------------------------|-------------------------|----------------------------|-------------------------|-------------------|
| 63.3 | 45.4 | 17.9 | 76.5 | 49.9 | 26.6 | 8.3 |
| 9.4 | 7.5 | 0.1 | 12.6 | 10.0 | 10.1 | 2.1 |

6.4.5 Nest Site Selection and Clutch size.

Six different tree species were observed being selected for nest sites. Five of these were *Eucalypt* sp, with one record of a nest in *Acacia dealbata*. This one record was from Maria Island off the east coast of Tasmania. A total of 68 records were analysed with regards to tree selection. Of these, 25 were records from field research and 43 from historic records. Figure 6.3 shows the proportion of tree species selected for nest sites. The use of *E. viminalis* was found to be significantly greater than other *Eucalypt* species ($\chi^2 = 53.618$, $df=4$, $p<0.001$).

The results obtained for other aspects of nest site selection indicate a preference for mature trees with a dense canopy cover. This allows nests to be suspended in the outermost foliage, but also ensures a relatively dense cover of leaves to camouflage and shelter the nest. The averages of other aspects of nest site selection measured are presented in table 6.2.

The average clutch size of *M. affinis* is 2.9 eggs ($n= 33$). Complete clutches range from 2 - 4 eggs. The egg itself is a small, pinkish in colour, with brown speckling (plate 6.4). Egg measurements are presented in table 6.3 ($n=54$).

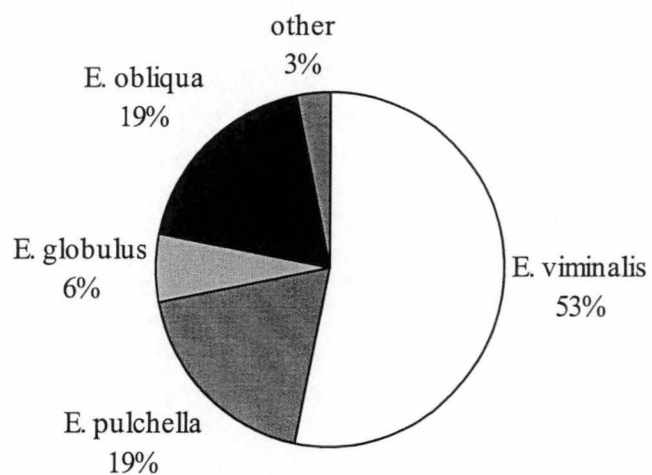


Figure 6.3 Plant species selected for nest sites by *M. affinis* across eastern Tasmania (n=68).

Table 6.2 presents the average measurements of five different factors measured with regards to nest site selection of *M. affinis*. Nest height is the only variable that combines historical and current field data. All other variables are field data only collected between 2000-2003.

| | Tree Height (m) | Nest Height (m) | Distance from central trunk (m) | Percent of foliage cover | Circumference of tree (m) |
|---------|-----------------|-----------------|---------------------------------|--------------------------|---------------------------|
| Average | 15.13 | 11.83 | 2.00 | 69.71 | 1.50 |
| SE | 1.57 | 0.56 | 0.52 | 4.87 | 0.38 |
| N | 17 | 68 | 17 | 17 | 17 |



Plate 6.4 *Melithreptus affinis* eggs

| | Length (mm) | Breadth (mm) | Circumference (mm) |
|--------------|--------------|--------------|--------------------|
| Average (se) | 19.55 (0.59) | 14.26 (0.47) | 44.80 (1.48) |
| Minimum | 18.2 | 13.2 | 41.47 |
| Maximum | 20.8 | 15.1 | 47.44 |

Table 6.3. Average length, breadth and circumference of eggs of *M. affinis*. Also presented are the minimum and maximum measurements. Data from Australian Natural Wildlife Collection.

6.4.6 Periods of incubation, nestling and juvenile dependence.

Due to the limited accessibility of the nests of *M. affinis* incubation and nestling periods are estimates, based on the behaviour of adult birds. It was not possible to establish laying dates of time interval between eggs laid, and so this aspect of breeding is not considered here. The estimated period of incubation for six nests observed from the beginning of the nesting period was 17.67 days (s.e. ± 0.27), ranging from 17 to 18 days ($n=6$). This is the period when adults are first observed to spend extended periods on the nest ($>10\text{min}$) to the first signs of adults feeding young, or the vocalization of juvenile birds, and thus indicate the longest possible period of the first hatched young.

Nestling period was calculated as being 15.4 days (s.e. ± 0.45 ; $n=5$), ranging from 14 days to 16 days. Figure 6.4 shows the timing of breeding in *M. affinis*, as well as the duration of different stages in the nesting period.

Five nests were observed as nestlings fledged. Young birds would move in

and out of the nest, wings flapping, with adults calling from some distance away. This behaviour would occur over extended time periods. All fledging instances were observed in the afternoon, with fledging occurring after 14:38 EST in nest RW300 and 15:15 EST in nest RW601.

There was no way to determine fledging period in this species, though observations suggest that this can be extended. In numerous instances, adult birds were observed feeding young birds that exhibited adult plumage, but still persisted with juvenile calls and begging behaviours.

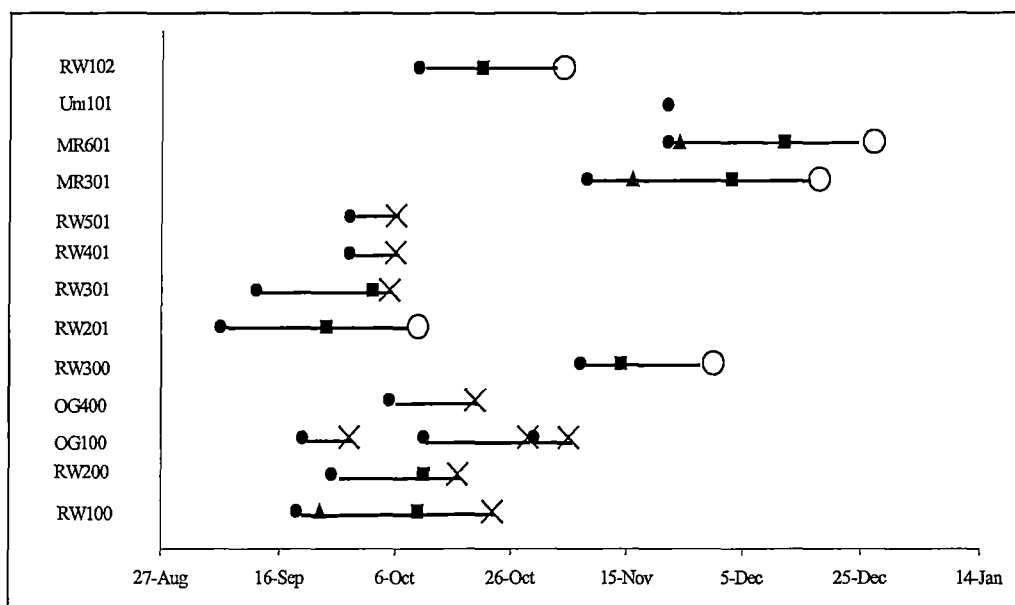


Figure 6.4 The timing of *M. affinis* breeding across all sites. An unbroken line represents one breeding attempt, closed circles indicate initial finding of breeding attempt, closed triangle indicates beginning of incubation, closed square indicates hatching. Successful nests end with an open circle, indicating fledged young, unsuccessful attempts are indicated with an X.

Hatching appears to be asynchronous, with distinct differences in plumage appearance and size of fledged birds noted. This may however, simply be natural variations occurring within the species.

Regression analyses were run on incubation length against both the natural log of weight and the natural log of egg volume of members of the Meliphagidae family. The data used in these regressions are contained in table 6.6, with results presented in chapter 9.

6.4.7 Reproductive Success.

Across the 42 nesting attempts recorded over three breeding seasons, 5 nests were built but never used, 2 were lost during incubation and 4 during nestling stage, 6 were followed through to fledgling, and 25 nesting records were found as fledglings.

Nesting success, defined as the production of at least one young from a nest, was 65.62%. This number was calculated from 42 nesting attempts over three years, where the outcome was known. This is believed to be a gross overestimate of the actual success, as many of the records used for analysis were of fledglings, which would undoubtedly bias the success rate. Using only the 17 nests that were found before fledging, this success rate is reduced to 35.29% of nests successfully fledging young. This value is much closer to that calculated using Mayfield's method, which gave a 31.3% success rate.

Success between seasons varies considerably, with the following success rates were calculated: for season 2000-01, 50% (n=12) of nesting attempts successfully fledged young, 2001-2002, 80% (n=25) of nesting attempts fledged young, and 2002-03, 100% (n=6) of recorded attempts fledged young. Again, these are overestimates, particularly so with the final breeding season. Over the six month breeding season, only 6 breeding attempts were recorded 2002-03, suggesting that a very low proportion of the population bred, and of those, only a small number actually produced viable young.

No significant differences were found between the numbers of fledglings across season, however there were significant differences in the actual number of nesting attempts ($\chi^2 = 13.163$, d.f = 2, $p=0.001$). Figure 6.5 Shows the total number of nesting attempts, total number of eggs laid and total number of fledglings found between the three breeding periods.

Egg success, defined as the chance an egg has of producing a fledgling, was calculated as 52.72%. For clutches where egg number was unknown, the average clutch size was used. Across season, the egg successes calculated were: 2000-01, 51.50%, 2001-2002, 53.50% and 2002-03, 68.03%. Again, these are probably over-estimates of the success within the population.

Success rates across seasons were not significantly different.

Data was unable to be collected that would allow an examination of the breeding cycles or recruitment of juveniles into the population. Banding data obtained for this species provides a coarse representation of annual recruitment. Figure 6.6 shows the proportion of juveniles of total banding records per year across the study region. This has been used to infer recruitment. There appears to be a pattern or cycle of a good season followed by a bad season, a pattern similar to that found in *Philemon corniculatus* and possibly a feature of honeyeater breeding (Ford pers. com.).

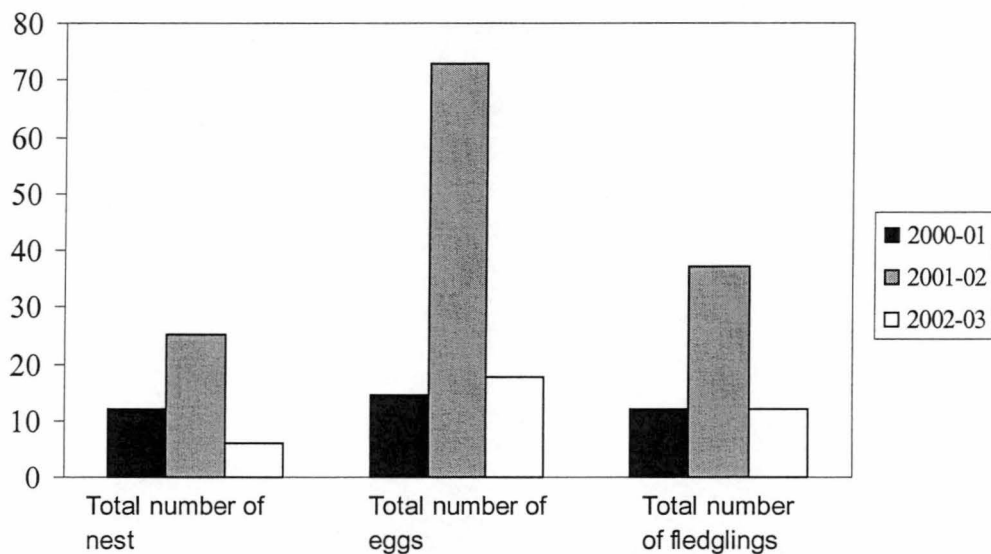


Figure 6.5 presents the total number of nesting efforts located throughout the study period, the total number of eggs potentially laid and the total number of fledgling encountered.

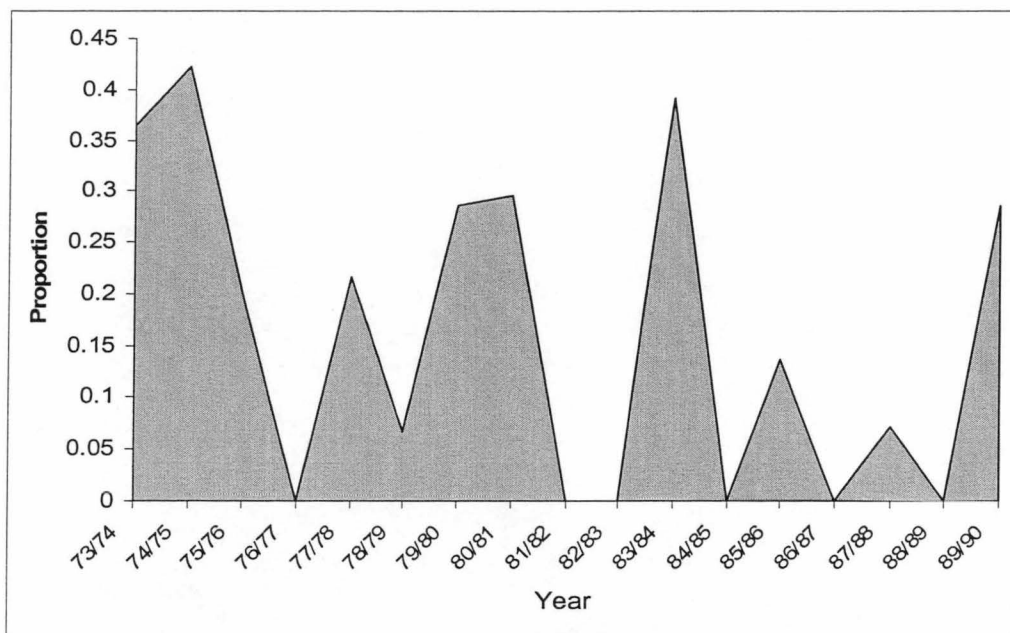


Figure 6.6 shows the proportion of juveniles trapped per breeding period between 1973 and 1990 across the study region. This data was provided by the Australian Bird and Bat Banding Scheme.

6.4.8 Re-nesting.

M. affinis has been recorded as being multi-brooded. Due to the inability to individually identify birds in this study, it was not possible to determine if birds re-nested after successfully producing young. It was possible to record the re-nesting attempts by unsuccessful birds. One pair re-built their nest three times during one breeding season (OG100, OG200 and OG300). Each of these nesting attempts was within 30m of one another. Each nest was built with the same material as the previous attempt, with the female meticulously removing the old nest to the new site. In this case, no juveniles were fledged from any of the nests. After the third re-nesting attempt, the birds disappeared from the area.

In a second instance of re-nesting, the initial nest failed at the nestling stage after an extended period of hot, dry weather (RW200). This nest was moved (again birds were observed removing nesting material from one site to the other) to a site 29 m from the original nesting tree (RW500). This second attempt was successful, with two young fledged.

Observations at UNI101 were of three birds during the construction of this nest. One of these birds displayed subadult plumage. This suggests that re-nesting will occur after successful breeding. This second nesting attempt was unsuccessful.

6.4.9 Co-operative Nesting.

Instances of co-operative breeding were definitely encountered, as were monogamous breeding strategies. Again, due to the inability to individually identify birds, in some instances it was not possible to determine the number of birds in breeding group. However, the simple fact that there was more than a breeding pair was inherently obvious. Nests RW200 and re-nesting attempt RW500 was a group of birds. Another two groups of fledglings were accompanied and fed by multiple adults. RW102, the only actual nest located in the 2002-03 breeding season, was a group of 3 birds, and a further two fledgling group in this season were also groups of adults. RW202, which managed to fledge three young, was a group of four adults. There were no obvious instances of co-operative breeding during the 2001-02 breeding season (other than the nesting attempt UNI 101 described above). There were no significant differences in the number of young fledged, or the proportion of fledglings from eggs laid between groups and individual pairs of birds.

6.5 Discussion

Before this study, the only first hand published accounts of breeding of *M. affinis* were those of Campbell (1901) and Brent (1905). Both of these publications are based on one or two nests. The RAOU nest record scheme, which has been used to elucidate the breeding of many of Australia's avifauna, received no records for *M. affinis* (HANZAB 2001) so subsequently, much that has been published on this species is based on the above two publications.

The results contained within this chapter necessitate changes to the literature available in the very basic aspects of breeding biology. To this date, breeding season has been assumed to be limited to three months, between October and

December. The results of this chapter indicate that the breeding period of this species is extended beyond late Spring and early Summer. Nesting events were most abundant in September and October, and extended through to February, lengthening the potential breeding period of *M. affinis* from three to six months. The ability of this species to breed is probably reflective of the environmental conditions at the time of initiation. As seen in Chapter 2 figure 2.1, the climatic conditions of Tasmania varied substantially between breeding periods. Subsequently breeding was initiated and concluded at different times. The first breeding period (2000-01) was initiated in September, with the latest record being fledglings found 23 January 2001. Breeding over 2001-01, again was initiated in September. In this case, fledglings were located in March, indicating the initiation of these nests being February. The final breeding period (2002-03), when breeding was poorest, extended from October to December. Evidence obtained in this study show nesting initiating in June (figure 6.1), and banding records also show the presence of juveniles in the population outside the above stated breeding period.

Bonding behaviour is similar in *M. affinis* to other species of honeyeater. Clarke (1988) described wing quivering and tail fanning in *Manorina melanophrys*, and Bruce (1988) described driving behaviour (where the male displaces a perching female) in *Lichenostomus flavicollis*. Both these behaviours were observed in *Melithreptus affinis*. Allopreening, an event where bonded birds preen one another, was also observed during the bonding process in *M. affinis*. Noske (1983b) noted a high level of physical contact within *M. brevirostris*, a trait he suspects typical of the genus. Courtship feeding was common in bonding *M. affinis* as well. The benefits of courtship feeding of the female by the male have been suggested as essential for the female to obtain enough nutrients to form eggs (Rowley 1975). Clarke (1988) who first described this behaviour in *Manorina melanophrys*, found instances of courtship feeding in this species was not necessarily for physiological benefit. There was evidence of mate guarding, where the dominant male inhibited feeding of his partner by other males, suggesting courtship feeding to be only used as a bonding mechanism (Clarke 1988).

Corrections to the literature (HANZAB 2001) need to be made with

regards to the nest building behaviour. Evidence from this study shows, that when a breeding pair build, the female does all the construction work. She is accompanied at all times by the male bird, though he never does any of the actual building. Whether this is consistent in co-operative situations is unknown as individuals were unable to be identified. In other co-operatively breeding honeyeaters, the breeding female does all the nest building (Dow 1978; Clarke 1988).

Unfortunately, as the nests measured were museum specimens, and the nature of placement of nests in the field, I was unable to pull any apart to consider the actual structure and amount of material used in construction. *M. affinis* is one of three species of birds in Tasmania to build pensile nests. The others are *M. validirostris* and *Zosterops lateralis*. It is hard to make comparisons between *M. affinis* nests and those of other species of honeyeaters due to the differences in the structure. *Phylidonyris pyrrhoptera*, *P. novaehollandida* and *L. mellanops cassidix* (of which data is available) all build cup shaped nests. Table 6.4 gives floor thickness and wall thickness of the above three honeyeater species as well as that of *M. affinis*. These measurements are taken from those given by Clarke & Clarke (2000). Measurements for *M. lunatus* taken from those given in HANZAB (2001).

Table 6.4 Floor and wall thickness of nests in four honeyeater species

| Species | Floor thickness (mm) | Wall thickness (mm) |
|--|----------------------|---------------------|
| <i>Phylidonyris pyrrhoptera</i> | 40.1 | 42.2 |
| <i>P. novaehollandida</i> | 24.4 | 36.5 |
| <i>Lichenostomus mellanops cassidix</i> (Summer) | ~8 | ~14 |
| <i>L. mellanops cassidix</i> (Winter) | ~14 | ~30 |
| <i>M. lunatus</i> | 20 | ~10 |
| <i>M. affinis</i> | 26.6 | 17.9 |

From these measurements it can be seen that the nest of *M. affinis* has thinner walls than other nests, but a deeper floor (except for that of *P. pyrrhoptera* which Clarke & Clarke 2000 suggest is a bulky nest for a bird its size). *M. affinis* shows a more robust nest than that of *M. lunatus* on the mainland.

This increase in depth (and subsequently increased weight), as well as the nest being able to swing, may allow the nesting bird better purchase, and the nest to remain upright during windy conditions encountered during the breeding period. This will decrease the chance of eggs, and later nestlings, being tipped out of nests. The depth in floor also provides nesting birds a base to hold. It has been noted on numerous occasions (particularly when nests are being collected, Campbell 1901; Brent 1905) that the nesting bird will still be sitting on eggs even after branches have fallen.

The selection of *Eucalyptus viminalis* as the major tree for nesting further shows this species dependence on this tree species. In chapter five it was seen that significantly more time was spent foraging in *E. viminalis* than other trees, a dependence noted upon by Longmore (1991). HANZAB (2001) however, does not mention this species of Eucalypt as being necessary for *M. affinis*.

6.5.1 Clutch size and egg size

There is no major difference between the clutch size of *M. affinis* and any other 'old endemic'. A clutch size of three is common amongst many of Australia's passerine species (Woinarski 1985a), with most honeyeaters having a modal clutch of two. A clutch of three appears to be the mode for *Melithreptus* sp. Egg size however, does increase in *M. affinis* compared to its congeneric mainland counterpart (table 6.5). This may be due to the slight increase in size of *M. affinis* compared to *M. lunatus*. However, increasing egg size in island populations is a trend seen in other species of birds in the Northern Hemisphere (Higuchi 1976; Wiggins *et al.* 1998). In some instances, this is believed to be related to an increased body size in the island populations (Higuchi 1976). However, in other instances (Blondel 1985; Wiggins *et al.* 1998), the island populations are significantly smaller in body size, but still show an increase in egg size. The suggestion is that reduced clutch sizes allows for greater investment in egg size and egg quality. Crowell & Rothstein (1981) suggest that as with clutch size, the variation in egg size is again related to food resource availability, not a reflection of egg quality.

Table 6.5 Comparison of egg size and clutch size between *Melithreptus affinis* and *M. lunatus*.

| | Weight (g) | Body length (cm) | Clutch size | Egg size (mm) |
|-------------------|------------|------------------|-------------|------------------------------|
| <i>M. lunatus</i> | 13-16 | 13.5 | 2.67 (2-3) | 19.4 (0.81) 13.3 (0.49) |
| <i>M. affinis</i> | 14-18 | 14 | 2.9 (2-4) | 19.55 (0.59) 14.26 (0.47) |

6.5.2 Incubation and nestling periods

Generally, incubation period and nestling period has been related back to the length of potential breeding season (Yom-Tov 1987). In Tasmania, Thomas (1974) suggested that the number of good breeding months available to Tasmanian avifauna was 4.5. This value was substantially smaller than for other areas of Australia; New South Wales 8.94, Victoria 8.33 and Queensland 5.58. This reduction in the number of good breeding months may be reflected in aspects of reproduction in Tasmanian avifauna, such as the time spent incubating and feeding young, as a breeding pair try to produce as many off-spring as possible over the shortened period. This principle is not being observed in *M. affinis*. The average incubation period of Honeyeaters across Australia is 14.06 days (Yom-tov 1987), ranging from 13-15 days (Ford 1989). For *M. affinis*, this period was found to last 17-18 days. Similarly, in *Lichenostomus flavicollis* in Tasmania, Bruce (1988) found an incubation period of 16-17 days, again, above the national average of incubation. However, although incubation is extended in *M. affinis*, the nestling period is not increased (table 6.5).

Comparatively, Thornbills have an incubation period of 17-19 days (Ford 1989), and Pardalotes 18-20 days¹ (Woinarski & Bullman 1985). The dietary requirements of these groups of birds are probably closer to that of *M. affinis* than other honeyeaters, as *M. affinis* is largely insectivorous (Thomas 1980; Slater 1994). These dietary requirements are consistent in *L. flavicollis*, which is also insectivorous (Slater 1994). Dietary requirements may only be one factor influencing incubation periods. Another factor that may cause this extension in incubation in *M. affinis* is a response to the climatic conditions to

which birds have adapted. Ricklefs (1993) after the careful measurement of temperatures, to which incubated eggs are exposed, suggested that this does not contribute to longer incubation periods. Extended incubation does appear to be related to a lower predation rates (Ricklefs 1993), and potentially lower brood parasitism. Ricklefs (1992) found that the prevalence of brood parasitism amongst adult birds decreases as the length of incubation increases. *Melithreptus affinis* has been strongly associated with brood parasitism by Pallid Cuckoos (*Cuculus pallidus*) (HANZAB 2001). The longer incubation seen in this species may have evolved in response to this brood parasitism.

Ford (1980) gives a 'probable' 14 day incubation period for *Melithreptus* sp, and 15 day nestling period. For *M. lunatus* these periods are 10-14 days and 14-16 days respectively (HANZAB 2001). This is reduced compared to that seen in *M. affinis* in this study. Differences in *Lichenostomus* sp. are also apparent (see table 6.6). A similar trend of an extended incubation periods is observed in *Pardalotus quadragintus*, another endemic Tasmanian species. This species has a longer incubation period than both its congeneric species, also found in Tasmania, but not endemic. However, *Phylidonyris novaehollandiae*, found across both Tasmania and mainland Australia, shows no difference in incubation length between island and mainland populations (Yuni 2002). Short incubation periods are associated with a high population growth rate, a characteristic found to significantly influence a species ability to invade (Duncan *et al.* 2001).

¹ Note that Pardalotes are hollow-nesters, which generally leads to longer incubation

Table 6.6 Incubation and nestling duration for Australian Meliphagids and small insectivorous species.

| Species | Weight (g) | Egg Volume (ml)* | Incubation Length (days) | Nestling length (days) | Source |
|---|------------|------------------|--------------------------|------------------------|-------------------------------|
| <i>Phylidonyris pyrrhoptera</i> | 14-17 | | 13.2 ± 0.2 | 13 | Clarke & Clarke 2000 |
| <i>Xanthomyza phrygia</i> | 43 | | 14 | 16 | Geering & French 1998 |
| <i>Manorina melanophrys</i> | 25-32 | 3.1 | 14.4 ± 0.34 | 11.7 ± 0.7 | Clark 1988 |
| <i>Conopophila albogularis</i> | 9-14 | | 14 days, 7 hrs ± 4.1 hrs | 14 ± 5.5hrs | Noske (1998) |
| <i>Lichenostomus mellanops cassidix</i> | | 3.0 | 14-16 | 11-13 | Franklin <i>et al.</i> (1995) |
| <i>Manorina melanocephala</i> | 70-80 | 4.5 | 16 | 16 | Dow (1978) |
| <i>Philemon corniculatus</i> | 92 | | 16.01 ± 1.0 | ≈16 | Courtney & Marchant (1971) |
| <i>Anthochaera carunculata</i> | 120 | 8.1 | 16-17 | 16-20 | Ford & Tremont (1999) |
| <i>L. flavicollis</i> | 22-40 | 3.0 | 16-17 | 16 | Bruce (1988) |
| <i>Melithreptus lunatus</i> | 13-16 | 1.8 | 10-14 | 14-16.5 | HANZAB (2001) |
| <i>M. affinis</i> | 14-18 | 1.9 | 17.67 ± 0.27 | 15.4 ± 0.45 | This study |
| | | | | | |
| <i>Acanthiza lineata</i> | | 1.2 | 16 | 18 | Woinarski (1985a) |
| <i>A. pusilla</i> | | | 17-21 | 15 | Woinarski (1985a) |
| <i>Pardalotus striatus</i> | 12 | 2.2 | >19 | >19 | Woinarski & Bulman(1985) |
| <i>P. punctatus</i> | 9 | 1.4 | >17 | 25 | Woinarski & Bulman (1985) |
| <i>P. quadragintus</i> | 10.7 | | 18-23 | 23-25 | Woinarski & Bullman (1985) |

* Egg volumes from Poiani & Jermiin (1994)

Incubation period is also believed to be related to the size (or weight) of a species, though Ricklefs (1993) indicates that egg volume is a more appropriate variable to consider when looking at length of incubation. Other factors of a species life history have also been found to correlate with incubation duration, such as increased laying interval and a long adult

lifespan. Though these traits were found to be restricted primarily to tropical and south temperate regions, they appear independently in a variety of taxonomic groups (Ricklefs 1993). The implications of a slower population growth rate and thus lower invasiveness are important in this instance, when considering *M. affinis*. This is an endemic island species, previously believed to have invaded the Tasmanian landmass at the end of the Pleistocene, along with all other modern avifauna. For this species to have successfully colonized at this point, life history traits needed to ensure rapid population growth and the ability to out compete other species. This is not characteristic of extended incubation. Is this characteristic indicative of a longer history in Tasmanian than previously considered? Does this indicate a similar history for other endemic species – that they have not ‘invaded’ Tasmania as it became isolated, but colonized the landmass when still attached to continental Australia? Is it simply a response to the climatic condition that Tasmania’s avifauna has been exposed too? It would be of worth to consider this aspect of breeding ecology with regards to other endemic species, as well as species of birds found across both Tasmania and the mainland.

6.5.3 Success

The reproductive success of *M. affinis* does not appear to be either larger or smaller than for other honeyeater species across Australia (table 6.7). However, it must be noted that the calculated values are probably an overestimate, due to the nature of the observation. Nest located at nestling stage or fledglings are more obvious, and so more likely to be located, biasing calculations to successful nesting attempts. Mayfield’s (1975) method corrects for the late finding of nesting attempts, and so for *M. affinis*, the Mayfield calculated value of 35.29% is believed to be more accurate than the 65.62% success calculated from raw values.

The small amount of literature comparing breeding success between mainland and island populations suggests a decrease in the success of island birds. Blondel (1985) and Blondel *et al.* (1993) found that in *Parus sp.* breeding success (defined as fledgling from nest) was significantly decreased on islands (such as Corsica) compared to mainland populations. Higuchi (1976) also

found that island sub-species had a lower breeding success than mainland counterparts, though the differences were not significant. Conversely, this island trend does not appear to be consistent in *M. affinis* which is showing comparable success rates to other members of the Meliphagidae family.

Table 6.7 Breeding success of various honeyeaters across Australia. Both raw data values (calculated as the number of nest from which young fledged) and Mayfield (1975) values are presented.

| Species | % Success (raw) | Mayfield (1975) | Source |
|---------------------------------|--------------------|--------------------|-----------------------------|
| <i>Phylidonyris pyrrhoptera</i> | | 20.1 | Clarke & Clarke 2000 |
| <i>P. novaehollandidae</i> | 36.8 | | McFarland 1986a |
| <i>L. mellanops cassidix</i> | | 39.2 | Franklin <i>et al.</i> 1995 |
| <i>Xanthomyza phrygia</i> | | 38.7 | Geering & French 1998 |
| <i>Conopophila albogularis</i> | 76 | 69.6 | Noske 1998 |
| <i>Philamon corniculatus</i> | 61 | | Ford & Tremont 1999 |
| <i>Anthochaera carunculata</i> | 77 | | Ford & Tremont 1999 |
| <i>Manorina melanophrys</i> | 43.6 | | Clarke 1988 |
| <i>Melithreptus affinis</i> | 65.62 | 35.29 | This study |

6.5.4 Co-operative breeding

The incidence of co-operative breeding in Australia is substantially higher than that worldwide, with 57 passerine species (22% of old endemics) of Australian species showing this life history strategy (Russell 1989). Comparatively, the rest of the world's avifauna shows only about 3% co-operative breeders (Brown 1987 cited in Russell 1989). Two main hypotheses have been developed to explain why there is such a high incidence in co-operative breeding amongst Australian avifauna. The first of these is that this life history strategy is in response to an erratic, unpredictable and often harsh environment, that undergoes large fluctuations in ecological condition; for example food abundance (Thomas 1974; Clarke 1995). The second broad explanation is that the aseasonal climatic conditions across the continent

in the past, and currently, has created conditions under which philopatric behaviour is likely to evolve (Clarke 1995). Subsequently, the profile of co-operatively breeding avian species tends to be sedentary, territorial and long-lived (Ford 1989). However, as with most ecological hypotheses, there are exceptions (eg: *Merops ornatus*, *Artamus cyanopterus*).

Co-operative behaviour in the Meliphagid family is quite common, with some species living permanently in colonies (eg *Manorina sp.*, Dow 1978; Clarke 1988; Poiani 1993), and others adopting this breeding strategy when necessary (eg *Phylidonyris novaehollandiae*, Clarke 1995, *Melithreptus brevirostris*, Noske 1983).

For *M. affinis*, the evidence suggests that this species does not breed co-operatively during periods of high resource abundance, but will switch breeding tactics under periods of environmental stress.

The climatic conditions over the period of this study fluctuated dramatically, with two periods of drought beginning and ending the study. Both these periods had a higher incidence of co-operative breeding observed than during the 'good' year. In the 2000-01 breeding period 3 incidences were recorded. Two of these three attempts were successful. Of the other 9 breeding attempts recorded for this period, 4 of these were nests that were never used and a 5th nest was lost at nestling stage. These attempts were all of breeding pairs. Similarly, when the impacts of drought were most harshly felt, the 2002-03 breeding period, where only six breeding attempts were located across the total six month period, four of these were of pairs plus extra birds. In one instance (RW 102) three birds fledged three young, for RW202 four birds fledged three young. MR102 was a record of a single juvenile in a flock of \approx 8 adults. The fourth record was of a pair of young, again with a large flock of adults.

Conversely to these two breeding periods, the breeding period 2001-02 had only one recorded instance of group breeding. This (as mentioned above in re-nesting) was an observation of a pair plus a sub-adult bird. They did not subsequently successfully nest. The other 24 records from this period were of pairs, who successfully fledged between one and three young.

It is considered that a response to the environmental conditions is driving the instances of co-operative breeding in *M. affinis*. Chapman (1995) also speculates that the co-operative breeding described for *M. gularis* by Dow (1980) is a response to environmental conditions, and subsequently may be used as an indication of the season stresses the species under goes in the Mount Lofty ranges. Co-operative behaviour has also been recorded for other species of *Melithreptus*. Noske (1983) described the behaviour at a nest for *M. brevirostris*. These birds were able to be colour banded, allowing for a definitive description of what was occurring. Dow (1980) also lists *M. lunatus* and *M. albogularis* as showing co-operative breeding. These species, like *M. affinis* are 'opportunistic communal breeders' (Dow 1980) where these behaviours may or may not occur from one year to the next.

6.5.5 Extended parental care

Russell (2000) reviewed the literature available on the time to independence of young, and concluded that for southern avian species, extended parental care played a major role in the recruitment of birds in to the general population. Thomas (1974) suggested that an adaptation to the Tasmania environment was delayed maturity of juveniles, and subsequent extended parental care, a hypothesis supported by Slater (1994). Though in need of further research, observations undertaken on *M. affinis* during this study period, would suggest that this is occurring in this species, particularly during harsh environmental periods. Towards the end of the 2002-03 breeding period, records were made of sub-adult birds (determined by the plumage), being attended upon by adults. The sub-adult birds continued with begging behaviour and juvenile calls, similar to those observed in recently fledged birds.

6.6 Conclusion

This chapter has reviewed and added to the scientific knowledge available on the breeding of *M. affinis*.

Environmental conditions were seen to substantially impact upon the breeding

of this species, with two of the three breeding seasons studied producing poor breeding records. Astheimer & Buttemer (2002) considered the hormone-environment aspect of breeding in Australian avifauna and how this relates to the environment. Such a study on *M. affinis* would quantify if indeed this species simply responds to environmental cues indicating a set breeding season or if, like other honeyeater species (eg *Lichenostomus pencillatus*, Astheimer & Buttemer 2002), it is able to re-initiate gonadal development when conditions such as rainfall or food abundance are favourable for breeding.

Characteristics such as extended incubation periods in Tasmanian endemics, the disparity between potential breeding periods and actual breeding season and extended parental care (Slater 1994) may be specific adaptations to the Tasmanian environment, potentially indicative of the time of invasion. These adaptations may be what have ensured the success of these species, where others have been unable to colonize. Most of the characteristics associated with breeding biology in island populations are not demonstrated in this species, providing evidence that at least for *M. affinis* the literature from Northern Hemisphere studies is not applicable in this instance.

7. PARENTAL BEHAVIOUR AND PROVISIONING EFFORT

7.1 Introduction

Parental behaviour, and the impacts of this on the rearing of offspring has long been an area of interest. Four general hypotheses have emerged from research into this aspect of avian biology (Silver *et al.* 1985). These are:

- The most prevalent pattern of sexual division of parental care among birds is a joint responsibility of both parents,
- The amount of parent care varies as a function of the mode of development of the young,
- The amount of male parental care depends on the mating system applied, and
- Dimorphism is often associated with a nonmonogamous mating system (Silver *et al.* 1985).

These characteristics were quantitatively tested and the relationship between parental care, mating systems, breeding biology and habitat characteristics were too strong to be attributed to chance (Silver *et al.* 1985). These characteristics allow us to begin to understand the complexity of mating systems and the implications for successful breeding.

In 1972 Trivers published writings on the conflict encountered between parent and offspring, providing a link between the breeding systems of an organism and their evolutionary benefits. Trivers (1972) concluded that it was the relative investment of the sexes in the young that was the key variable controlling the process of sexual selection. When one sex invests more in offspring, then the other will compete more frequently among themselves for multiple mating opportunities (Trivers 1972). Parents are classically assumed to allocate time to offspring in such a way as to maximize reproductive output, whilst offspring are assumed to be passive vessels into which adults pour appropriate care (Trivers 1974). This however, is not necessarily the case and has led to the idea of parent-offspring conflict.

Parent-offspring conflict is basically the notion that parents can and will

invest in their offspring at a level that will result in the most number of viable offspring with the least impact upon themselves. The offspring however, demand a greater level of commitment, placing pressure on parents to provide above and beyond what they can efficiently sustain. The conflict arises when the offspring demand more than the parent can sustain. This can be further exacerbated with the introduction of multiple offspring, leading to competition between siblings for parent attention (Godfray 1995). It is theorised that this changes the balance with the benefits to the offspring approaching equilibrium with parental benefit (Lazarus & Inglis 1986). This conflict can intrude upon many aspects of the reproductive process and while theoretically plausible, there is some suggestion that it is very rare in nature (Godfray 1995).

The focus of this chapter is on one aspect of this potential conflict, that of the time parents commit to the provisioning of food to offspring.

For animals that exhibit parental care, one of the major considerations is the provisioning of young. Subsequently, the life history strategies imposed by a species must ensure not only the young survive, but the adults as well.

Over 90% of all birds exhibit a monogamous breeding system (Goodey & Lill 1993), with some degree of biparental care demonstrated. Trivers (1972) suggested that as females are predisposed to provide parental care (since they have invested already in the production of eggs), paternal care becomes crucial to reproductive success. Male involvement in nesting activities in monogamous non-passerines is common, but less so in passerines (Goodey & Lill 1993). Subsequently, much of the research on this aspect of life history has been focused on non-passerines that show extreme life history traits such as Procellariidae (Petrels, Shearwaters and Prions) (Hamer *et al.* 1998; Granadeiro *et al.* 1999; Baduini 2002).

Within Passerines, research has been undertaken on those species that show unusual breeding systems. In the case of Dunnocks (*Prunella modularis*) this species shows extreme variation in mating systems, displaying polygyny, polyandry, polygynandry or monogamy (Davies 1986). It is this variability in mating systems and subsequent provisioning that has the greatest

influence on reproductive success (Davies 1986). For Australian terrestrial avifauna, research has been undertaken on the co-operatively breeding fairy wrens (Peters 2002; MacGregor & Cockburn 2002), babblers (Brown *et al.* 1978) and Kookaburra (Legge 2000). Two species of flycatcher have also been considered and show the other extreme, where both parents invest the same amount of energy into offspring after the initial egg production (Goodey & Lill 1993; Tremont, & Ford 2000). This increased paternal care has been positively associated with the certainty of fathering the offspring (Moller 1988).

The provisioning of offspring is a factor that has relevance to all avian species, whether they are terrestrial, monogamous or multi-brooded. The aim of this chapter is to quantify provisioning efforts of adult Black-headed honeyeaters, and the time commitments made to breeding efforts. What drives the frequency for adults to feed their young has generally been considered a response to some signal from the offspring, whether it is calling intensity (McGregor & Cockburn 2001), offspring size or fat content (Baduini 2002). Brown *et al.* (1978) and Luck (2001) suggest that the rate at which juveniles are fed is reflective of other environmental factors including brood size, temperature, season and time of day. The external factors of diurnal period and drought periods are explored in this chapter to determine if they have an effect on the duration of incubation bouts in *M. affinis*, and feeding bouts of both brooding adults and juveniles and to determine the frequency of these bouts.

7.2 *Methods*

A comprehensive outline of the methodology applied has been described Chapter 2.

Through detailed observations records were made of the time at which incubating birds returned to nests and began bouts, of the time at which they left nest, ending a bout, and the time at which other adults attended the nest whilst incubation was underway. Similarly, during nestling and fledgling periods, records were taken of feeding visits, the duration of these visits

and the time interval between adults feeding young.

Due to the inability to individually identify birds, the provisioning rates of males and females and thus the parental care given within *M. affinis* is not able to be considered, and so data has been broken down into breeding season, nest stage and diurnal variations.

For the stages of incubation and nestling, observations totalling an hour were taken per diurnal period. These periods were grouped as morning (sunrise to 1030) mid day (1030 to 1430) and afternoon (1430 to sunset). Subsequently, three hours of recorded observations were taken per stage for each nest if possible. In some instances nests were found too late in the incubation stage to allow for this data to be collected, and similar situations occurred during the nestling stage. In some instances nest were lost before the completion of a stage, so again, the total data were not able to be collected.

In the fledgling stage, data were collected whenever fledglings were located, with observations being continued for as long as possible. As the fledged young of *M. affinis* are quite mobile after fledging, moving out of nest territories within days of fledging (pers. ob.), it was difficult to continue the observations of nests after this point. This difficulty is compounded by the inability to catch and mark birds, so fledgling were assumed to be from an observed nest for as long as the remained in proximity to the nest site, and within a few days of fledging.

The duration of feeding visits to nest sites are used as an indirect measure of the quantity of food being provided to young. Though this is imprecise, due to the nature of nests, no other method of measuring quantity of food being given to young is possible, and it stands to reason that a greater quantity of food being given to young would take a longer period of time to distribute than a smaller quantity.

7.2.1 Data Analysis

Rather than calculate frequency as the number of visits to a nest per hour by an adult, the time interval between nest visits was calculated and this value was used to assess differences in the frequency of feeding bouts for nestlings

and fledglings. This method provides more comprehensive ecological information than simply the number of times an adult attends a nest over a set time period. The same method was employed to calculate the frequency of incubation bouts.

Raw data was tested for normality and found to violate assumptions. Data was natural log transformed, providing a normal distribution. Once transformed, Two-factor ANOVAs with unequal replications (Zarr 1999; Coakes & Steed 1996) were used to determine if significance occurred between incubation frequency, feeding frequency of nestlings and fledgling and duration of incubation, nestling feeds and fledgling feeds with diurnal period and between non-drought and drought periods. Data were pooled across sites, as this was not found to significantly effect any of the periods being tested. Similarly, there were no significant differences found to occur between individual nesting attempts, again allowing the pooling of data. To test if significant differences occurred in the frequency of provisioning to nestlings and duration of feeds between the beginning of the nestling period and the end, One-way analysis of co-variance (ANCOVA) was used to correct for the effects of drought conditions on the provisioning rates. This method was also applied for comparisons between nestling and fledgling stages.

All statistical procedures were undertaken using SPSS 10.0 computer software.

7.3 Results

A total of 1736 mins of observations were collected across 18 nesting attempts during three breeding seasons. Of these nesting attempts 6 nests had data collected for the duration of the nesting cycle, 6 were of fledglings only and the remaining 6 were lost at various stages through the cycle. Incubation and nestling stages were determined by the behaviour of adult birds at the nest due to the location of the nest sites (see previous chapter for descriptions).

7.3.1 Incubation bouts and incubation feeding.

Observations suggest that the female is predominately responsible for the incubation of eggs. It was possible to identify sexes in some instances by the presence of a brood patch in some females. Also the size discrepancy between male and female birds (see chapter 3) made it possible to identify gender when pairs attended nests. When pairs attended nests, it was always the smaller of the two birds that actually climbed onto the nest to undertake incubation bouts. However, it was observed that the male would relieve the female at the nest for short periods.

On average, incubation bouts were initiated every 13 mins 42 secs (s.e. \pm 3 mins 7secs), or 4.79 (s.e. \pm 0.47) times in an hour. These bouts lasted 9 mins 31 secs (s.e. \pm 1min 3secs). Average time off the nest was 4mins 3 secs (s.e. \pm 54 secs). When tested for diurnal variations, neither the duration of incubation bouts nor frequency of incubation bouts were found to significantly vary (figure 7.1a). It can be seen that although not significant, there is a trend of increasing time between incubation bouts, thus a decrease in the frequency of incubation throughout the day, coupled with a decrease in the duration of incubation bouts. Drought had an effect on the duration of incubation bouts (figure 7.1b), with a significant decrease on the length of bouts during periods of reduced rainfall ($F_{5,65} = 13.525$, $p=0.002$). Table 7.1 presents periods of time allocated during drought and non-drought periods for frequency of incubation and duration of bouts.

Incubation feeding was observed to occur at some nests, though not frequently enough to warrant statistical analysis. This behaviour was observed at nest RW200 and RW300, that is two nests at the same site during the 2000-01 breeding period. This breeding period was affected by reduced rainfall, and subsequently this behaviour may be reflective of that. It may also be reflective of co-operative breeding, with an increase in the provisioning to the incubating female by other members of the group. However, due to the inability to individually identify birds at nest sites, this is only a suggestion.

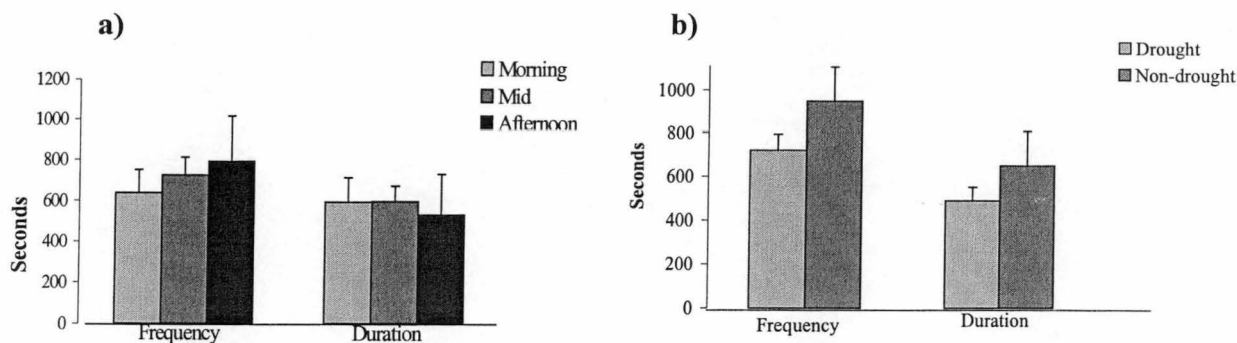


Figure 7.1a shows comparisons of time between incubation periods and the duration of these periods across diurnal periods. Morning is sunrise to 10:30am, Mid 10:30am – 2:30pm, Afternoon 2:30pm to sunset. **b** compares the frequency of incubation periods and the duration of incubation periods between periods of reduced rainfall (drought) and periods of normal or increased rainfall (non-drought).

7.3.2 Nestling Period

Once eggs had hatched, the energy of adults committed to their young increased. Unlike incubation, where the female commits more to the offspring than the male, during the nestling period both adult birds contribute to the feeding of nestlings. Nestlings were fed at a frequency of 3 mins 27secs (± 18 secs), and lasted a period of 10.8secs (± 0.48 secs). This equalled 18.4 ± 2.43 feeds an hour. Across diurnal periods, there was no significant variation in the interval between feeds; however, as is shown in figure 7.2a, the effort by adult birds is reduced during the morning period, with greater time lapsing between feeding bouts. As with incubation, there was a significant variation in the frequency at which nestlings were fed during drought affected periods. Provisioning of nestlings was decreased during drought periods (table 7.1, figure 7.2b) with significant differences in the time interval between consecutive feeding bouts ($F_{5, 213} = 4.108$, $p=0.044$). For feeding visits where the gender of the adult was able to be determined, 50% were female and 50% were male ($n=12$).

Table 7.1 provides average frequency and duration of incubation, nestling provisioning and fledgling provisioning. Statistical comparisons are between drought and non-drought periods. $p<0.05^*$, $p<0.01^{}$, $p<0.001^{***}$**

| | | Incubation | Nestling | Fledgling |
|-----------|-------------|---|-----------------------------------|---------------------------------|
| Frequency | Drought | 11mins 58secs (\pm 1mins 13 sec) | 3mins 50sec** (\pm 24secs) | 2mins 3secs (\pm 17secs) |
| | Non-drought | 15mins 47secs (\pm 2mins 25sec) | 2min 15 secs** (\pm 17secs) | 1min 54 secs (\pm 31secs) |
| | | | | |
| Duration | Drought | 8mins 10 secs** (\pm 1min 1sec) | 10.78secs (\pm 0.53sec) | 6.59secs (\pm 1.21secs) |
| | Non-drought | 10mins 49sec** (\pm 2mins 39secs) | 12.42 secs (\pm 1.91secs) | 6.18secs (\pm 0.88secs) |

Though not significant, feeding bouts was found to occur more frequently as the nestlings became older (figure 7.2c), though again, duration of feeding bouts did not differ. This increase in frequency of feeding is observed into the fledgling period, again, with the time between feeds significantly decreasing as offspring become older ($F_{2, 316} = 15.387$, $p<0.001$). The duration of feeding bouts also significantly reduces between the two nesting stages ($F_{2,291}=52.735$, $p<0.001$), from 11secs \pm 0.68sec during nestling period to 6 secs \pm 0.98secs once fledged.

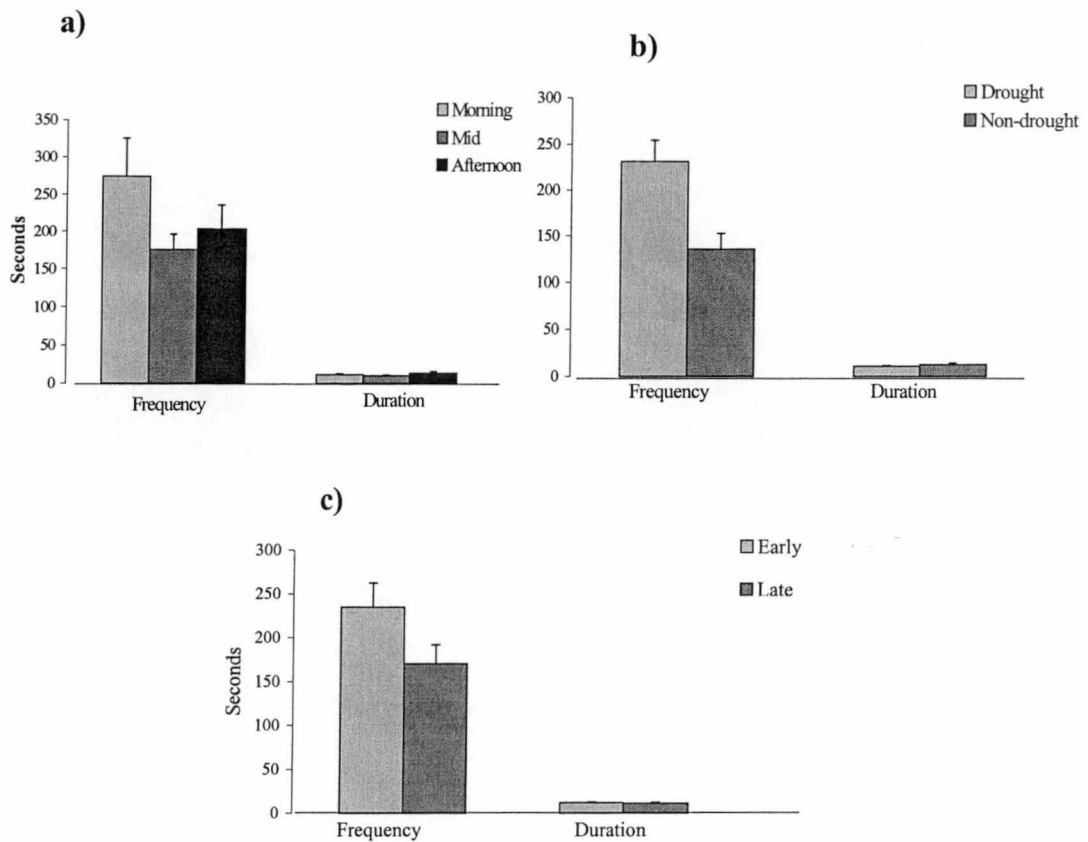


Figure 7.2a shows the frequency and duration of provisioning bouts during the nestling stage. Morning, mid and afternoon are as in figure 7.1a. b shows variation between drought and non-drought periods, and c compares the first half of nestling period (early) with the second half of the nestling period (late).

7.3.3 Fledgling period.

Of the fledgling groups observed, 52% were of two fledglings, 26% of a single fledgling and the remaining 24% of three fledglings. There were no significant differences in frequency and duration of fledgling provision with diurnal or drought period (figures 7.3a and b).

After fledging, juvenile birds would huddle together for the first two-three days after leaving the nest. After this point, birds would increase in mobility, with juveniles moving throughout foliage and foraging themselves. In 82% of records, adults fed only one juvenile per feeding bout ($n = 75$). In some instances, when adults foraged in close proximity, it was ascertained that each adult took on the provisioning of specific juveniles. When pairs were provisioning two young, each adult attended to only one offspring. All fledgling instances observed during this study were of three young leaving

the nest, though the frequency of three fledglings being provisioned was found to be uncommon. It may be that generally only two young survive, perhaps reflecting the input of adults to the provisioning of off spring. In the instance of nest RW102 where three young were observed to fledge, in returning to the vicinity of the nest territory within five days of the fledging day, only two young birds were able to be located. Though not individually marked, it is believed that these birds were those from the located nest as no other birds were found breeding in the area where young were located. No other nest records were made during the 2002-03 breeding season. On average, fledglings were fed every 1 minute 59 secs (± 15 secs), for the duration of 6 secs (± 0.98 secs), equating to 26.6 ± 5.3 feeds in an hour.

The frequency and duration of feeding was calculated for a brood of one, two and three to determine if parental investment differed with brood size (figure 7.3c). A single fledgling was fed every 1 minute 23 secs (± 28 secs) for a duration of 6 seconds (± 0.8 secs), individuals of a brood of two were fed every 2 minutes 10 secs (± 21 secs) for a duration of 8 secs (± 1 sec) and individuals of a brood of three were fed every 1 minute 51 secs (± 19 secs) for a duration of 6 secs (± 0.6 sec). Neither frequency of feed or the duration of the feed showed significant variation with brood size. Total feeding effort, calculated as frequency x duration, did not significantly vary with brood size.

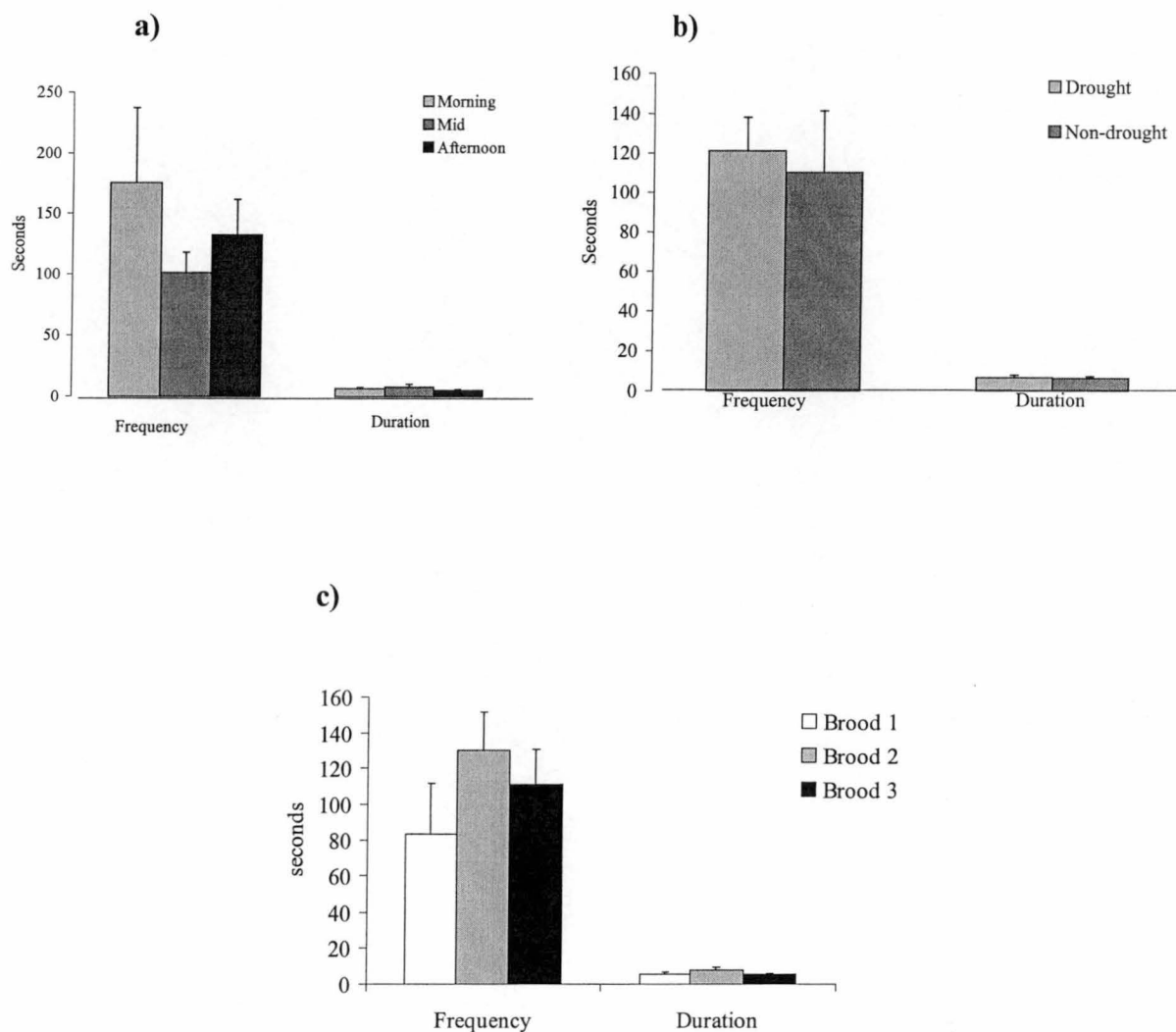


Figure 7.3a shows the frequency and duration of provisioning bouts during the fledgling stage. Morning, mid and afternoon are as in figure 7.1a. b shows variation between drought and non-drought periods. c shows the variation between brood size

7.4 Discussion

The frequency at which *M. affinis* was found to provision nestlings was similar to that found in the Brown-backed Honeyeater *Ramsayornis modestus* – one visit every three minutes (Maher 1996). However, *R. modestus* is a tropical honeyeater species, and although both species provision at similar rates an hour (*R. modesta* 20.3 visits (Maher 1996), *M. affinis* 18.4), when considering day length (the tropical species only working 11 hours and the

temperate working up 17 hours) the feeding effort undertaken by *M. affinis* becomes greater than the tropical honeyeater species. Compared to other temperate species, frequency of feeding per hour is still increased in *M. affinis*, with species such as *Passer domesticus* (House Sparrow) provisioning at a rate of 15 times an hour (Seel 1969), and *Dendroica discolor* (Prairie warbler) also feeding at a rate of 15 times an hour (Nolan 1978 cited in Maher 1996). Potentially, *M. affinis* has greater energy requirements and commits more to the rearing of offspring than other species, with an increase in the number of feeding visits to nest over a longer day length. These values however, do not consider the brood size of the study species. Observations would indicate that for most nests two - three nestlings are being provisioned, as these are the most common numbers of fledged young observed (this does not take into account juvenile mortality). Subsequently, the differences in brood size may account for variation in provisioning between *M. affinis* and other temperate species. Substantial changes have been recorded for many species in the rate at which adults provision off-spring and the number of young being provided for. In *Climacteris rufa* (Rufous Treecreeper) provisioning rates increased by up to ten visits an hour when two nestlings were being care for, as opposed to a single juvenile (Luck 2001). *Dacelo novaeguineae* (Kookaburra) show significant increase in the amount of food received by nestlings when brood numbers increased; larger broods received significantly more food (Legge 2000).

The allocation of time to juvenile birds in *M. affinis* shows a significant interaction with environmental conditions. Years when rainfall was reduced, were found to significantly alter the duration of incubation bouts and significantly reduced the frequency at which nestling were fed. Both these behavioural changes are believed to be in response to a reduction in the availability of appropriate food resources. Due to the reduction in food, incubating females had to forage for themselves over a greater period of time to obtain the necessary energy requirements to ensure its survival during this period. This did not appear to impact upon the successful hatching, as nests from which data were collected during periods that were drought impacted all successfully hatched young. It was not possible to determine the number

of eggs laid or the subsequent number of eggs that hatched, so there is some potential that not all eggs laid produced successful young.

The second significant impact of reduced rainfall was that of a reduction in the frequency at which nestlings were fed, though the duration of these feeds, potentially an indirect measure of the quantity of food provided, did not change. Again, if food availability is sparser, then it is probable that the time taken for adults to collect an appropriate amount of food for nestlings will be increased, thus increasing the time between feeds. Harvest time, that is the time it takes for adults to collect food and return to juveniles, has been found to contribute positively to the provisioning rates of juvenile birds (Kacelnik & Cuthill 1990). It has been found that allocation of food to juveniles by adults increases with harvest and brood size. This allocation is at the expense of the adult and could affect numerous aspects such as the parent's own food intake, resting time, safety or the quality of diet (Kacelnik & Cuthill 1990). Whatever the mechanism that establishes the costs in breeding, it is likely to involve parental condition and parental decisions (Slagsvold 1984; Smith *et al.* 1987).

In Procellariiformes, unpredictable pelagic food sources are a common occurrence, and thus species have developed methods to compensate for this (Granadeiro *et al.* 1999), for example nestling obesity (Hamer *et al.* 1998). It is conceivable then that birds within other environments will have mechanisms in place should unfavourable conditions be encountered. During extreme conditions, as experienced in the third breeding period of this study, it was found that in *M. affinis*, rather than limit the adult investment in offspring, the species simply did not breed. The second breeding period, where rainfall was increased, and conditions more favourable did not show the same frequency of co-operative nesting. During this period only one re-nesting attempt had an extra bird present.

Where nestling starvation limits productivity, related helpers can enhance productivity (Legge 2000). Thus helping during periods of drought in *M. affinis* may be a mechanism to ensure productivity and reduce nestling starvation. In most published studies, the overall effect of helpers is to

increase the overall provisioning levels. Helpers have also been implicated in reducing the effort invested by primary breeders (Dunn & Cockburn 1996; Magrath & Yezerinac 1997), subsequently reducing the energy commitments to juveniles, increasing the adult's potential survival.

If there is an increase in the occurrence of co-operative breeding in *M. affinis* during periods of environmental stress, one could argue that the significant difference in the frequency of provisioning to nestlings should not occur, as extra adults allow the provisioning rate to remain constant. That is the extra provisioning should be additive. This, however, is not the case in *M. affinis*, with a decrease in the rate of feeding encountered when co-operative breeding is more common. This has been found to occur in other species. Brown *et al.* (1978) concluded that in Grey Crowned babblers (*Pomatostomus temporalis*) the benefit to parents and nestlings from a helper does not arise from a greater rate of feeding the nestlings. Rufous Treecreepers (*Climacteris rufa*) have also been found to have compensatory provisioning by extra birds, rather than an additive effect (Luck 2001).

As juveniles age, the frequency at which parents provide food for their young increase. This trend is seen across a range of species such as *C. rufa* (Luck 2001) and *D. noveahollandidae* (Legge 2000). This behaviour is consistent in *M. affinis*. *Malurus cyanus* show a similar trend, with provisioning increasing as juvenile age (Dunn & Cockburn 1996). This is believed to be in response to the increased frequency of vocalization in offspring (MacGregor & Cockburn 2002). The evidence presented by such authors as Godfray (1995) and MacGregor & Cockburn (2001) that as young age they become more vocal, inducing a greater effort in the provisioning rate of adults, is applicable to *Melithreptus affinis*. Though not considering specifically the vocalization of juveniles in this study, it was noted that juveniles became more vocal as they aged, and this may explain why a significant increases in the frequency of feeding was found after juveniles fledged. Interestingly, the time spent attending upon juveniles decreased with this increase in frequency, with no differences when one two or three young were being fed. If duration is taken as an indirect measurement of food quantity, then *M. affinis* is providing significantly less food to fledged young than those in the nest.

Observations of fledglings found that fledged young would forage independently of adults (though the age of fledglings was unknown), but continued to demand food from adults birds. Although feeding was more frequent to fledged young, this may have been at the expense of size or quality of prey (Whittingham & Robertson 1993, MacGregor & Cockburn 2001), which is compensated for by juveniles foraging for themselves.

M. affinis is typical of monogamous, altricial birds with regards to gender roles and the input into nesting (Silver *et al.* 1985). Females undertake most of the building and incubation of eggs, with males contributing to incubation in the way of courtship and incubation feeding. The role of courtship and incubation feeding has been theorized to be correlated with the 'nest attentiveness' of the female and potentially overall success. Hatupka (1994) found that incubation feeding increased in *Anthus pratensis* (Meadow Pipits) at the expense of reproductive success, suggesting that for this species, incubation feeding is a type of insurance – the intensity increases when the clutch is threatened by unfavourable conditions and the female has high energetic demands (Hatupka 1994). This may be similar in *M. affinis*, where incubation feeding was only encountered in nests during drought periods. However courtship feeding was encountered across all seasons, and may provide vital food resources in preparation for the breeding of the female. During periods of environmental stress, incubation was found to be reduced in duration, with females leaving the nest more frequently for significantly longer periods, presumably to forage on limited resources.

Once eggs have hatched, both the female and male share the provisioning of juveniles, with variations again being observed with periods of environmental stress. During drier periods, *M. affinis* provisioned nestlings less frequently, but the duration was the same as periods of advantageous environmental conditions. This suggests that on each visit to the nest a similar amount of food was given to young, but due to environmental conditions more time was spent foraging as greater effort was needed for adults to maintain themselves (possibly at the expense of the offspring) and harvest the desired quantity of food for nestlings. Diurnally, provisioning was least frequent in the morning, possibly reflecting the need of the adults to obtain necessary energy

demands owing to food deprivation overnight (Luck 2001). After this period, there is an increase in the frequency of provisioning, where adults provide energy requirements for nestlings.

7.5 Conclusion

Parental investment by *M. affinis* is consistent with other monogamous species, with the female investing most in the early stages of the breeding and male birds assisting after incubation. As offspring age, the effort of adults increase, making the contributions of the male birds imperative for successful juvenile production. The results of this study show also that, as suggested by Brown *et al.* (1978) and Luck (2001), environmental conditions have an effect on the provisioning of juveniles. *M. affinis* altered provisioning rates in response to environmental conditions, possibly implementing co-operative breeding strategy during periods of suboptimal environmental conditions.

8. CLASSIFICATION AND GEOGRAPHIC VARIATIONS IN THE VOCALIZATIONS OF *MELITHREPTUS AFFINIS*

8.1 Introduction

Most species of bird can be identified by call with a small amount of practice by a naturalist. There is a long history in the study of bird song, with studies dating back into the 1770's exploring the song learning process (Barrington 1773 cited in Slater 2003). Within each species, differentiation between call type may be ascertained, and the function of these calls understood (McDonald 2001). Subsequently, bird calls have been used to attack a wide range of behavioural questions such as inter/intra specific interactions (Slater 1993), predator responses (Wood *et al.* 2000), mate selection and reproductive success (McGregor *et al.* 1981; Wasserman & Cigliano 1991; O'Loughlen & Beecher 1999; Lampe & Espmark 2003) and cultural evolution (Baker *et al.* 2000; Payne *et al.* 2000; Baker *et al.* 2003) resulting in theoretical and technical advances (Slater 2003).

Vocalizations have been applied to studies in the evolution of morphological traits. Island birds which show size variations show vocal differences, with the smaller island species producing shorter, higher frequency calls than the larger mainland species (Doutrelant *et al.* 2001).

These morphological variations are consistent within other birds. In a study on the distress calls in Australian passerines and non-passerines, Jurisevic and Sanderson (1998) found that body size significantly influences the call produced. The larger the bird, the longer and louder the call, with lower

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External parameters also show an influence on the calls of some birds. There is a body of literature confirming the role of the physical environment (Liskens *et al.* 1976; Hunter & Krebs 1979), and geographic location (Rogers 2003) on the development of calls. Sound transmission through different environmental conditions varies with impacts upon both song attenuation and signal degradation (Handford 1981; Slabbekoorn & Smith 2002). Background noise, such as that encountered within an urban environment, has

also been shown to influence the calls of birds, with Great Tits (*Parus major*) increasing the frequency of the mating calls, to ensure they are heard above the urban noise (Slabbekoorn & Peet 2003). These habitat variations may in part account for the geographic variations recorded in many species (Slabbekoorn & Smith 2002). Geographical differences in calls within avian species have also been attributed to cultural differences in discrete populations where certain songs are learned (Mundinger 1982).

Thus, the vocalizations of birds are more than simple songs. Calls are a reflection of morphology, environment, culture and the selective pressures of reproduction. This study takes the first step in unravelling the vocalizations of *M. affinis* in Tasmania. The first aim of this chapter is to define and classify the vocalizations of *M. affinis* and determine the behavioural associations of these calls. Secondly, call types recorded across the south east of Tasmania will be compared to determine if geographic variations occur within the physical parameters of *M. affinis* calls. There has been no attempt to determine dialect variation (defined by Warren (2003) as sharp boundaries between discretely varying forms of a signal) in this study, as individual identification was not possible.

8.2 Methods

8.2.1 Field recordings.

To determine if the calls of *M. affinis* vary with location, calls were recorded from unbanded birds across 9 different field locations. These can be seen in figure 8.1. Calls were recorded between February 2001 and April 2003, incorporating both breeding and non-breeding periods. As calls were recorded, observations were made of behaviours displayed when vocalizing. These notations extended to non-recorded birds to provide a larger sample group.

Calls were initially recorded using a Sony TC- D5m Capstan Server Stereo Cassette recorder, with a Nikamich CM – 300 condenser microphone with CP-4 shot gun attachment. The cassette recorder was replaced with a Sony

Portable Minidisc recorder, MZ – N707, with the same microphone, which was lighter and more compact for field work, mid way through 2002.

As calls were recorded onto minidisc they were in digital format from the initial recording, reducing the loss of sound quality through the downloading process. Calls originally recorded with the cassette recorder were recorded onto minidisc before being downloaded onto a computer. A standard PC was used for computer analysis (Celeron, 128M RAM, 20gig hard drive), and minidisc was connected through the microphone port on the hard drive.

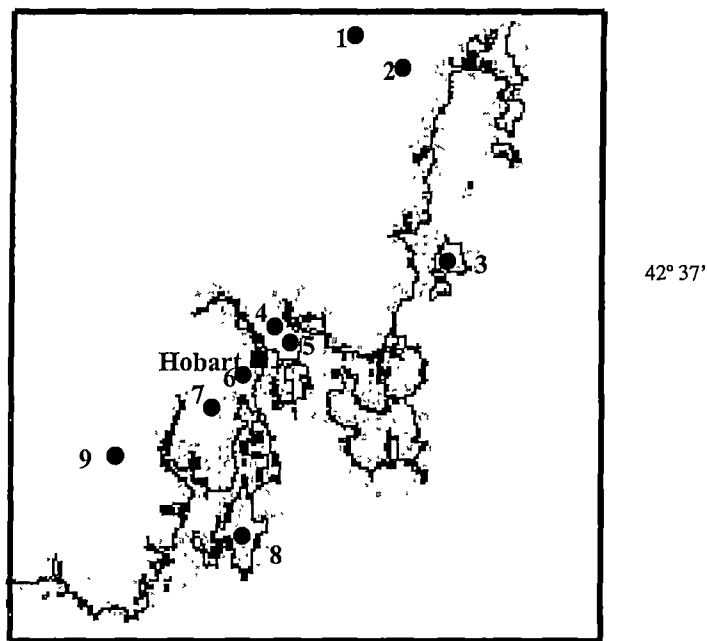
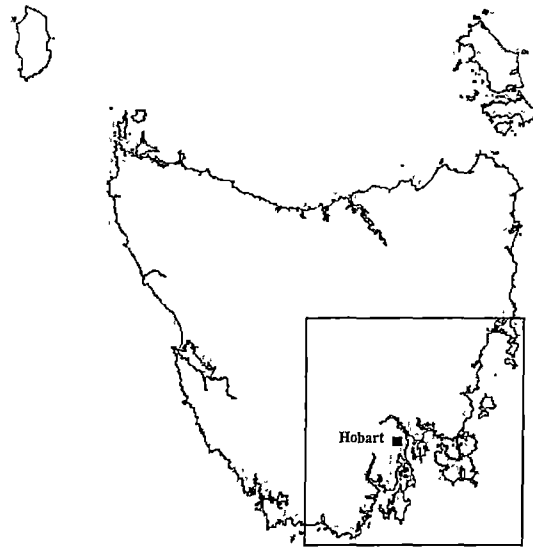


Figure 8.1 Map of locations where calls were recorded. Numbers correspond to the following locations: 1 Lake Leake; 2 Lost Falls Reserve; 3 Maria Island; 4 Mount Direction; 5 Meehan Ranges; 6 Ridgeway (and University Reserve); 7 Allens Rivulet; 8 Bruny Island (South Island); 9 Tahune Forest Reserve

8.2.2 Song analysis

Recorded calls were fed directly into the computer program Syrinx (John Burt, www.syrinxpc.com) to generate spectrograms. These were produced to allow measurements of the parameters of calls to be taken (figure 8.2).

For each relevant syllable displayed on a spectrogram the following variables were measured in order to analyse vocalizations. These variables were chosen as they encompasses the major variables of the calls and as this was the first analysis of this species vocalization there are no records of the significant parameters and so it was felt all parameters should be measured and tested for significance.

The variables measured were (see figure 8.2):

1. Beginning time of syllable
2. End time of syllable
3. Syllable length (secs)
4. Between Syllable time (secs)
5. High frequency (KHz)
6. Low frequency (KHz)
7. Band width (KHz)
8. Beginning frequency (KHz)
9. End frequency (KHz)

For calls where harmonics occurred, the strongest signal was measured, with a record taken of the number of harmonic peaks (Kentish *et al.* 2001). Any peaks or troughs encountered in syllables were also noted, with a record taken of the frequency of the peak or trough, plus the time at which the change occurred, allowing for the time interval between the beginning of the call and the peak/trough to be calculated.

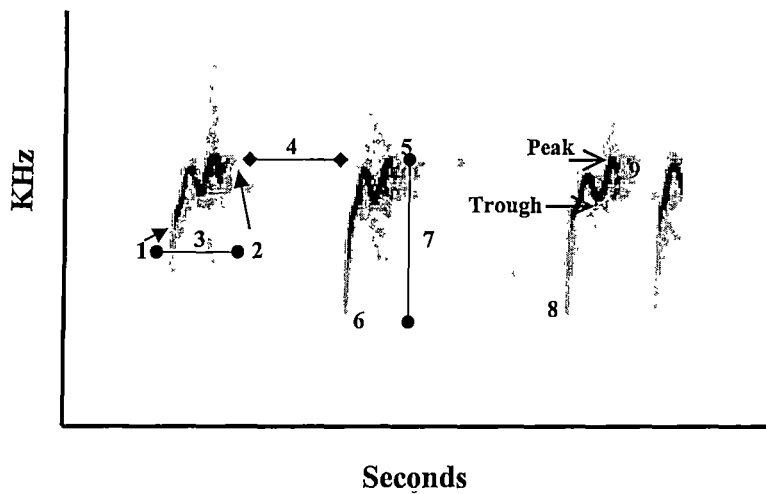


Figure 8.2 Spectrogram indicating the variables measured for each syllable used in the analysis of *M. affinis* vocalizations. 1-9 correspond with the variables listed in the text above.

Three levels of classification were applied to the vocalizations recorded, and analysis was undertaken at each level. These classification levels were:

1. Call: allocated by visual classification of spectrograms (Tracy & Baker 1999) and sound of call, combined with an knowledge of the behavioural traits associated with the production of the vocalization.
2. Phrase: the finite vocalizations of individuals within each call type. These ranged from single to multi-syllable phrases. The term phrase has been applied rather than *song*, as song is generally used to refer to the breeding calls of males.
3. Syllable: the individual components that an individual vocalizes that make up a song.

8.2.3 Statistical Analysis

Detailed descriptions of each of the statistical procedures used in this chapter have been described in chapter 2.

For each of the call types defined, Principal Component Analysis (PCA) was applied to determine which of the measured variables contributed most to the variation in songs (Field 1996). An exploratory approach was taken to allow for the most variance to be explained. Once initial components were isolated, the significant variables were rotated using varimax orthogonal rotation to ensure that significant variables were defined (Pallant 2001).

Once the variables that contributed the greatest were defined, they were used for further analysis.

A grand mean for each variable for each individual song was calculated, and analysed using Multivariate methods. Multidimensional scaling (MDS) was applied to determine the overall similarities in each song to one another.

Variation in the individual parameters measured was tested across site using MANOVA to determine if geographical variations occurred in the physical characteristics of *M. affinis* vocalizations.

All tests were undertaken using SPSS 10.0.

8.3 Results

8.3.1 Call Definitions.

Seven call types were able to be isolated within the calls recorded across sites. Of these seven, sample sizes and call quality allowed for four call types to be specifically defined and analysed. These are described and classified as follows:

Call Type one (figure 8.4): Typical “shirp” call uttered in quick succession (as in the spectrogram) or in singular or paired syllables. This call is utilized interspecifically to drive off potential predators/threats such as Kookaburras (*Dacelo novaeguineae*), Grey Shrike-thrush (*Colluricincla harmonica*) and Black Currawongs (*Strepera fuliginosa*). The call is characterized by the arc shape with the call finishing on a lower frequency than it started from. Harmonics occur above and below the main level, and can number up to 3 above and below.

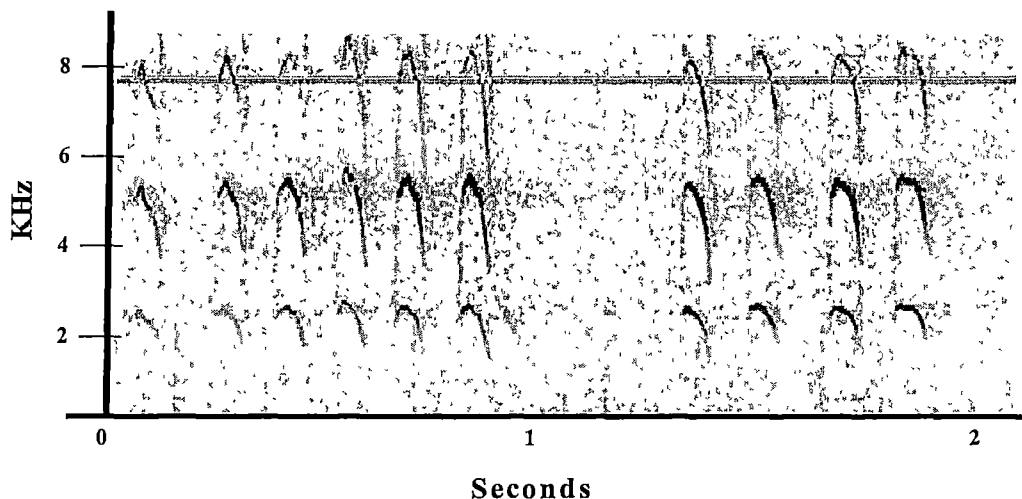


Figure 8.4 Call type 1, recorded at Allens Rivulet.

Call type two (figure 8.5): Territorial call during the breeding period, and is used by individuals (generally males) to establish and defend nesting territories. The call is a distinctive, sharp whistle. When the territory is invaded by another *M. affinis* the female will also emit this call if the male can not expel the interloper on his own. This call is characterized by a reverse 'S' shaped syllable generally repeated in quick succession, and may be started with an 'n' shaped syllable. The first syllable of the spectrogram presented in figure 8.5a may be uttered without the rapid trill that follows, but be repeated at either the same or a higher frequency. This change in frequency was most encountered within the Bruny Island calls

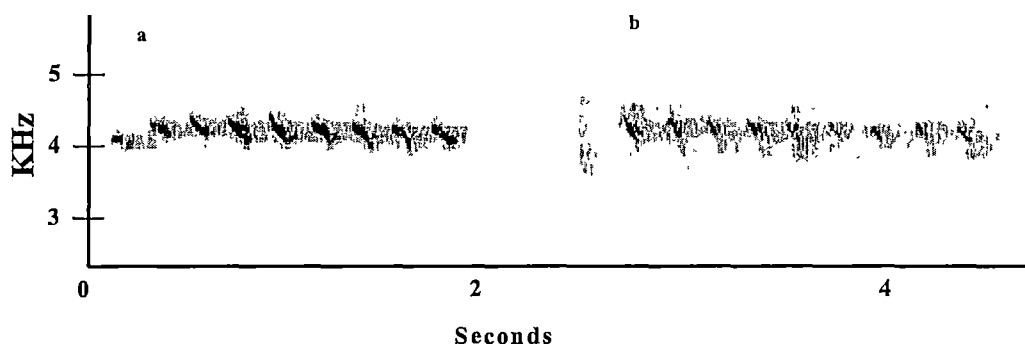


Figure 8.5 Call type 2 a) recorded at Ridgeway, b) Meehan Ranges

Call type three (figure 8.6) is an inflight contact call, emitted generally as individuals are in flight. This call is characterised by a decrease in frequency from start to end over a wide band width, and is again a sharp, strident call.

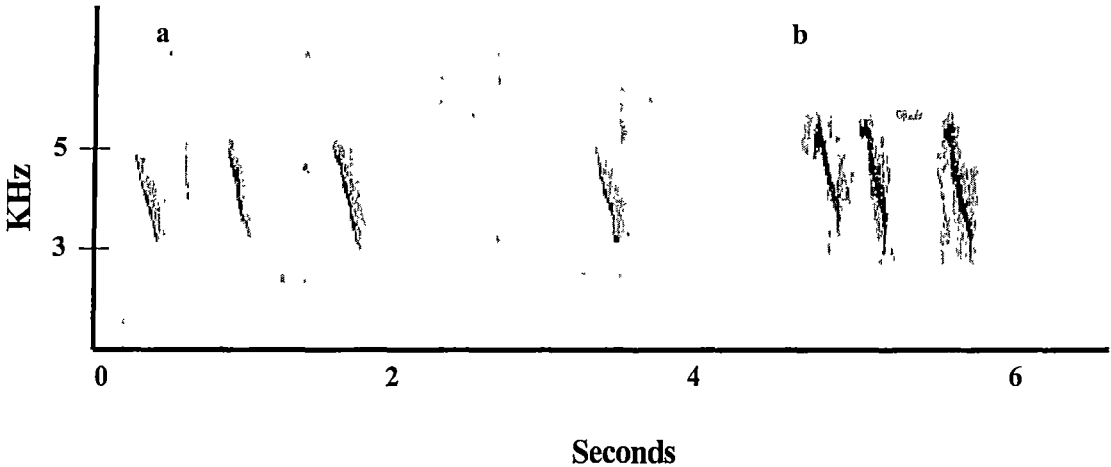


Figure 8.6 Call type 3 a) recorded at Meehan Ranges, b) Recorded at Mount Direction

Call type four (figure 8.7) is the distinctive ‘squeaky’ call of the study species. It is characterized by an ‘M’ or ‘N’ shaped spectrogram, beginning with the low frequency of the call, peaking with the highest frequency. This call may contain numerous syllables, but is equally as common as a single uttered squeak. Again, this appears to be a contact call, probably used within flocks, due to the lower frequency and lower amplitude of the call. The presence of harmonic bands also occurs with this call type.

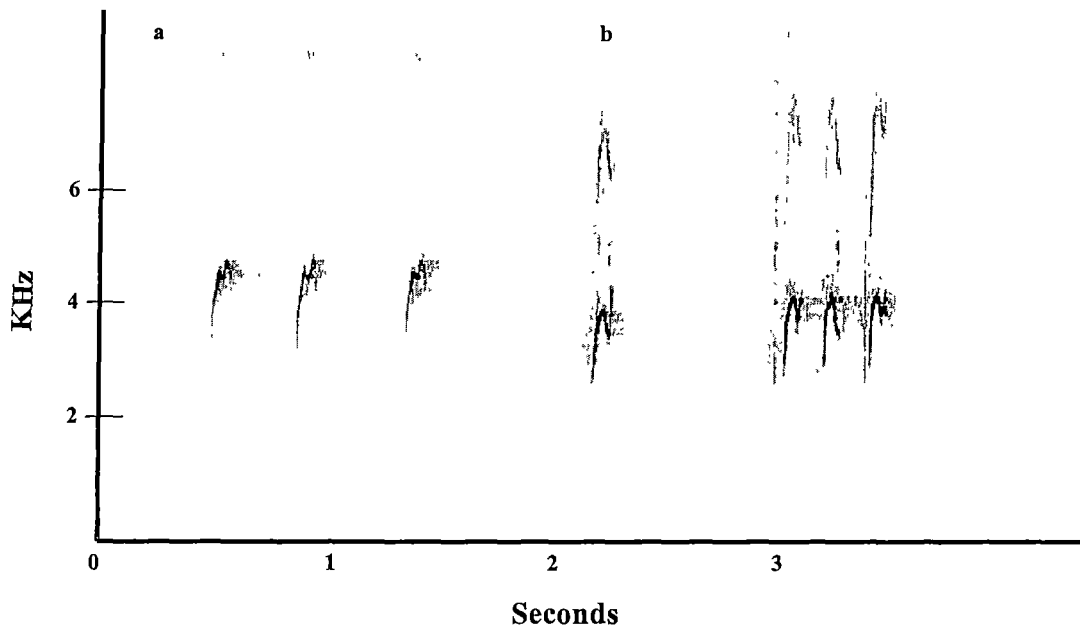


Figure 8.7 Call type 4 a) recorded at Ridgeway, b) recorded at Mount Direction

Three other calls were found to occur across some sites. These calls were not analysed, but spectrograms are provided for these call types (figure 8.8, 8.9).

8.3.2 Phrase Analysis

A total of 447 individual songs were recorded across the study period across all sites. Not all call types were recorded for each site. Of these, 72% ($n=322$) were placed into the four call types described above. When coming to analysis, some phrases were discarded due to the quality of the call and subsequent spectrograph quality. In total, 245 individual songs were analysed across the four call types (76% of the total number of phrases allocated to the four call types). These were allocated as follows: call one 78 phrases; call two 62 phrases; call three 58 phrases and call four 47 phrases.

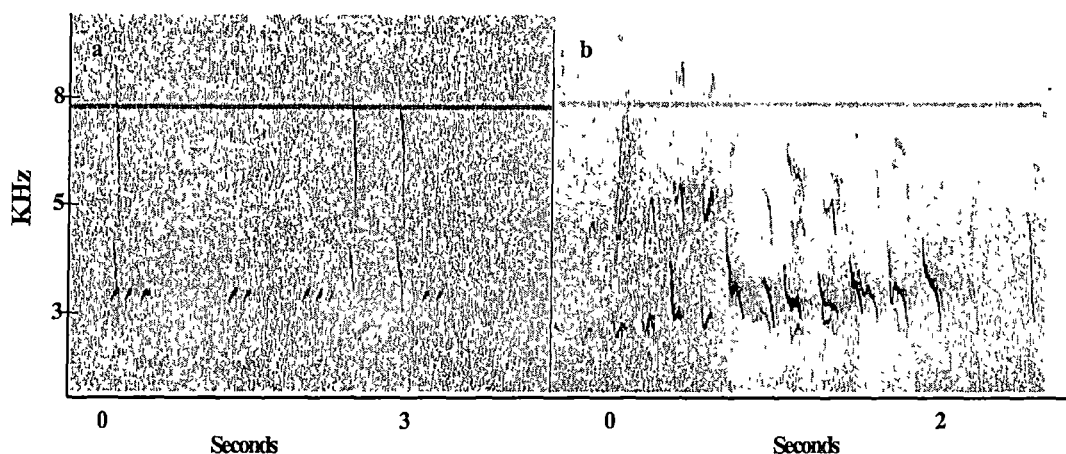


Figure 8.8 Two call types defined but not analysed. Call a) was recorded at Allens Rivulet (the low frequency triple calls are those of *Pardalotus striatus*) and has a whinging tone to the call. This call seems to be produced by younger, submissive birds, or in the case of a breeding pair, the female. b) recorded at site Meehan Ranges is a lower frequency 'babble'.

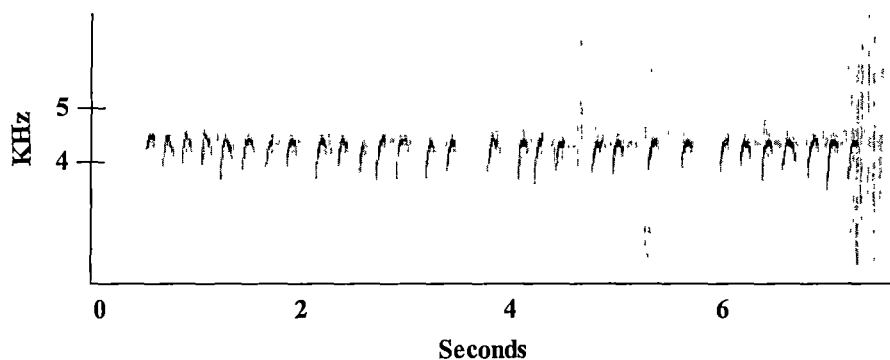


Figure 8.9 Alarm call of *M. affinis* recorded at site Ridgeway

Table 8.1 provides the results of the PCA for the four calls and the subsequent variables used for the further analysis of phrases. For call type one, six variables were found to explain 81.3% of the variation encountered within phrases. Call types two, three and four were explained by five variables, totalling 81.8%, 97.1% and 99.6% of variance consecutively.

Table 8.1 Results of PCA with variables found to significantly contribute to variation in calls presented. Also presented is the weighting calculated by the PCA.

| Variable | Component | | |
|---------------------|-----------|--------|--------|
| | 1 | 2 | 3 |
| Call 1 | | | |
| High Frequency | .941 | | |
| Low Frequency | .909 | -.356 | |
| Bandwidth | | .888 | |
| Harmonics below | | | .936 |
| Harmonics above | -.494 | | .738 |
| Duration | | .709 | |
| % Variance | 32.749 | 24.708 | 23.926 |
| Call 2 | | | |
| High Frequency | .862 | .469 | |
| Low Frequency | .957 | | |
| Bandwidth | | .981 | |
| Beginning Frequency | .799 | | |
| End Frequency | .707 | | |
| % of Variance | 55.925 | 25.845 | |
| Call 3 | | | |
| High Frequency | | .971 | |
| Low Frequency | .977 | | |
| Band Width | -.801 | .588 | |
| Beginning Frequency | | .950 | |
| End Frequency | .977 | | |
| % of Variance | 51.512 | 45.585 | |
| Call 4 | | | |
| High Frequency | .496 | .646 | .578 |
| Low Frequency | .914 | .362 | |
| Bandwidth | -.469 | .312 | .826 |
| Beginning Frequency | .956 | | |
| End Frequency | .318 | .904 | |
| % of Variance | 46.330 | 30.552 | 22.727 |

These variables were used for the subsequent analysis of phrase and syllable variation.

Figures 8.10 – 8.13 show the resulting MDS plots for each song type.

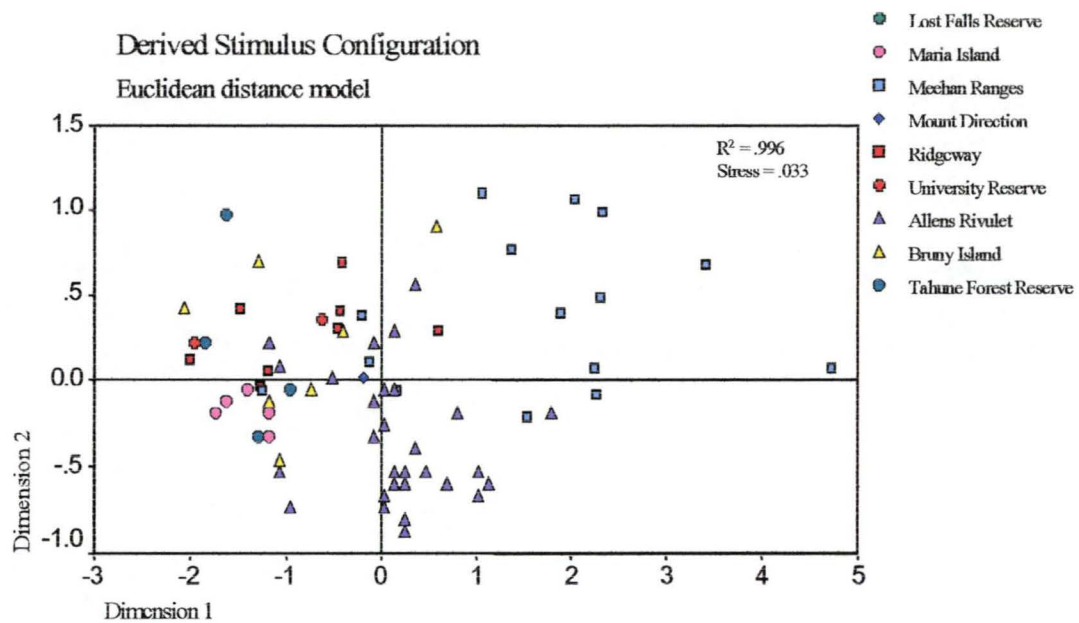


Figure 8.10. MDS of means of variables for the songs classified in call type one.

The MDS for call type one (figure 8.10) shows general grouping of phrases based on site. The phrases of the Meehan Ranges (4 on figure 8.1) tend to separate from the rest of the phrases. The Allens Rivulet phrases (7 on figure 8.1) also form a group apart from other phrases. The phrases from Maria Island (3 on figure 8.1) clump together, though overlap in spatial distribution with phrases from other locations.

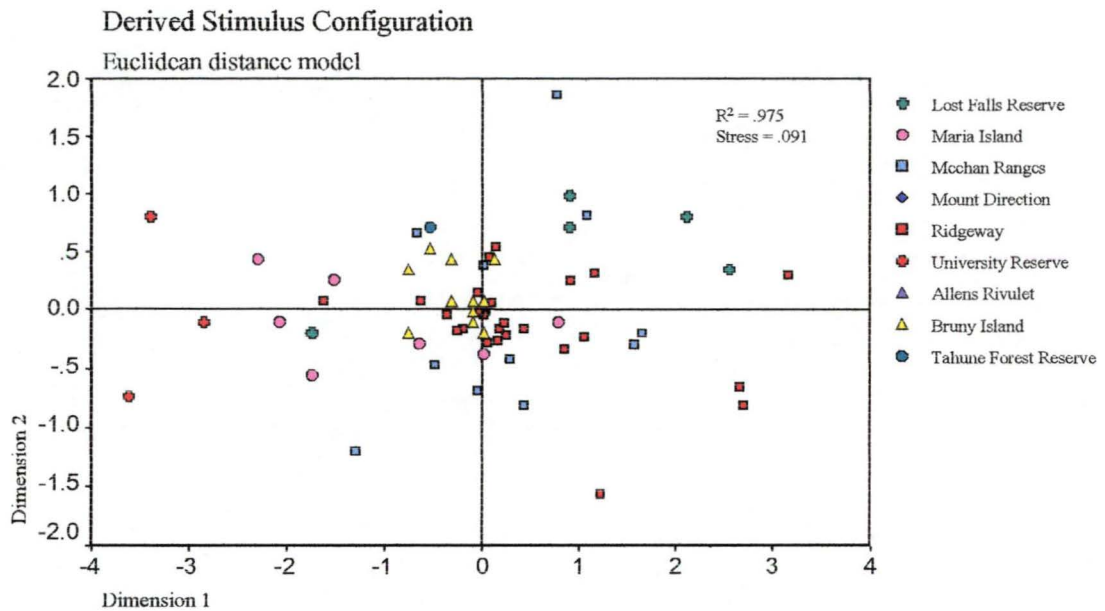


Figure 8.11 MDS of means of variables for phrases classified as call type two

Figure 8.11 again shows clumping of phrases (call two) with geographic location. The phrases recorded at University reserve (6 on figure 8.1) separate from the main clump of phrase points. The nearest geographic location to this site is Ridgeway. These phrases form two main groups – those tightly grouped at the centre of the plot and a group of four on the far right of the plot. This indicates variation within sites between individual phrases, particularly in this call type, which is a breeding call.

Again, the phrases of the Meehan Ranges form a distinct group for call three (figure 8.12). This group overlaps with the phrases of Mount Direction (4 on figure 8.1), with the calls of Maria Island again generally grouping together.

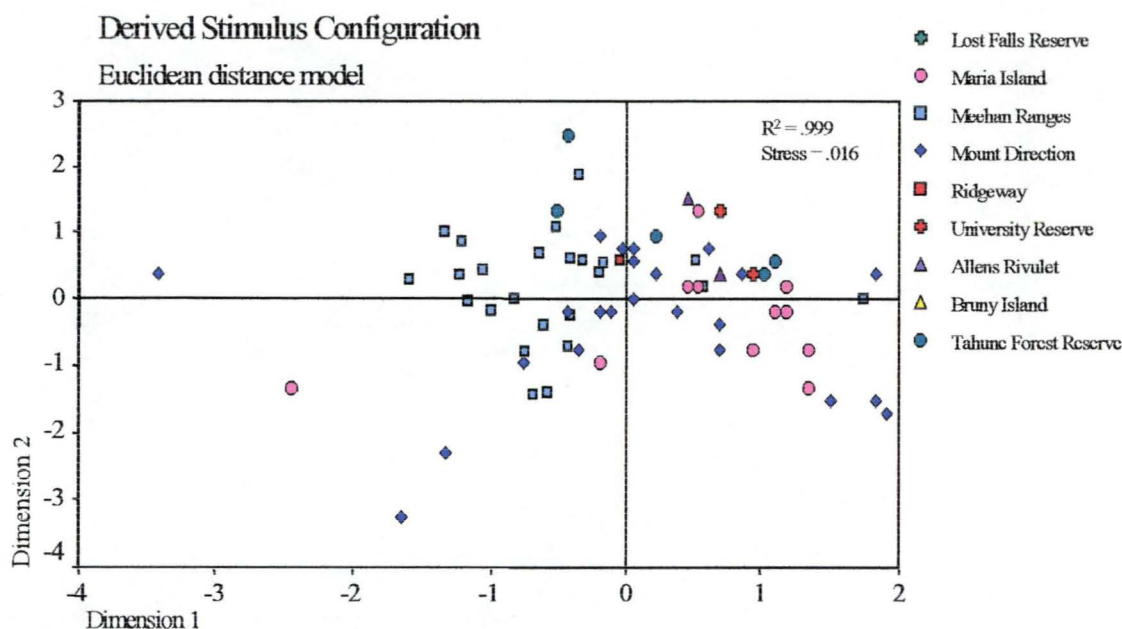


Figure 8.12 MDS of means of variables for songs classified as call type three

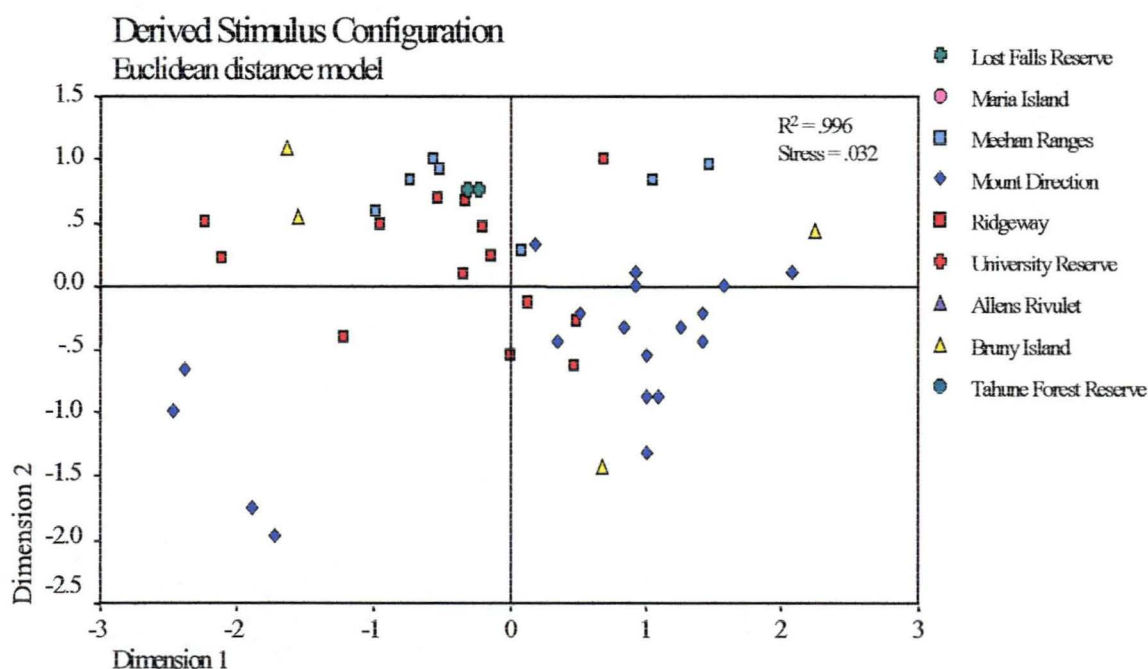


Figure 8.13 MDS of means of variables for songs classified as call type four

Call four suggests a distinct phrase type restricted to Mount Direction, with a small group forming to the extreme left of the MDS plot (figure 8.13). A second group from this site forms with the majority of songs clumping in this

group. Bruny Island (8 on figure 8.1) also shows differences in calls to other locations. The songs of Bruny Island, Meehan Ranges, Ridgeway and Allens Rivulet show a similar trend of a main clump (or more similar songs) with a secondary group forming at a great distance from the main group. The most obvious of these are the songs of Mount Direction. The main group of these are to the right of the plot, with a small group of four songs forming to the extreme left. These calls to the left separate out, again because of a difference in the maximum frequency reached, with them being around 7KHz compared to the other calls reaching a peak around 5 KHz.

8.3.3 Site variation in syllable parameters

Individual syllables were measured to determine parameters of the vocalizations of *M. affinis*. Figures 8.14a – d graphically show the variation in the mean values for each syllable parameter with site. The actual values for these parameters are provided in appendix 3. Statistically significant variations were found to occur with almost all parameters across sites for each of the call type (table 8.2). For calls two, three and four there is a north/south trend occurring with frequencies increasing the further south the site. Call one shows an increase in frequency in calls recorded at the University Reserve site, and then drops off, with frequency increasing southward. For three of the four call types, the syllables recorded at the Meehan Ranges are seen to occur at a frequency lower than other sites. For calls one and two, these differences are found to be significantly lower (table 8.2). Conversely to the Meehan Ranges calls, the syllables analysed from the University Reserve reach a significantly higher frequency than encountered across other sites. Recordings for this site are small in sample size however, and may not be an accurate representation of the syllable repertoire of birds at this site. Parameters measured from Tahune Reserve calls show differences at this site are also generally significantly higher than other sites. For call type one, both the high frequency and low frequency are significantly higher than five other sites. Call one (figure 8.14A) shows a north/south variation with generally a higher maximum frequency found at the more southern sites. Bruny Island differs from this southern group with a lower frequency more similar to the

northern sites. Similar trends are seen in the low frequency records across sites. The other major difference that can be seen across these figure is that of the significantly lower frequency encountered in call four at the Mount Direction site. Though no difference is occurring with the high frequency of this call, there is a dramatic difference in the low frequency of these calls. This is found to be significantly lower than all other calls.

Table 8.2 Significant variation for each call parameter tested across geographic location. * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$ Not all calls were recorded across all nine sites.**

| Variable | Call type one | Call type two | Call type three | Call type four |
|---------------------|-----------------------------|-----------------------------|----------------------------|-----------------------------|
| Duration | $F_{7, 536} = 9.846^{***}$ | | | |
| High Frequency | $F_{7, 536} = 49.551^{***}$ | $F_{6, 264} = 11.734^{***}$ | $F_{6, 166} = 6.676^{***}$ | NS |
| Low Frequency | $F_{7, 536} = 46.562^{***}$ | $F_{6, 264} = 14.400^{***}$ | $F_{6, 166} = 4.369^{***}$ | $F_{4, 163} = 14.796^{***}$ |
| Band Width | $F_{7, 536} = 24.314^{***}$ | $F_{6, 264} = 10.356^{***}$ | $F_{6, 166} = 5.479^{***}$ | $F_{4, 163} = 17.398^{***}$ |
| Beginning Frequency | | $F_{6, 264} = 13.473^{***}$ | $F_{6, 166} = 5.110^{***}$ | $F_{4, 163} = 16.648^{***}$ |
| End Frequency | | $F_{6, 264} = 4.523^{***}$ | $F_{6, 166} = 4.369^{***}$ | NS |

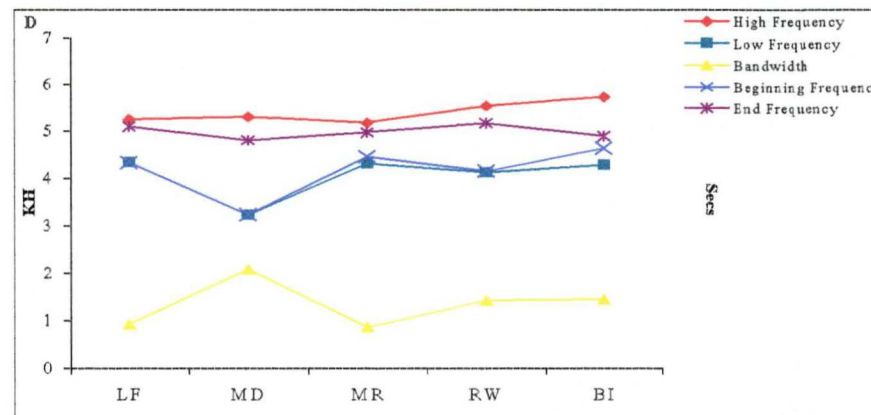
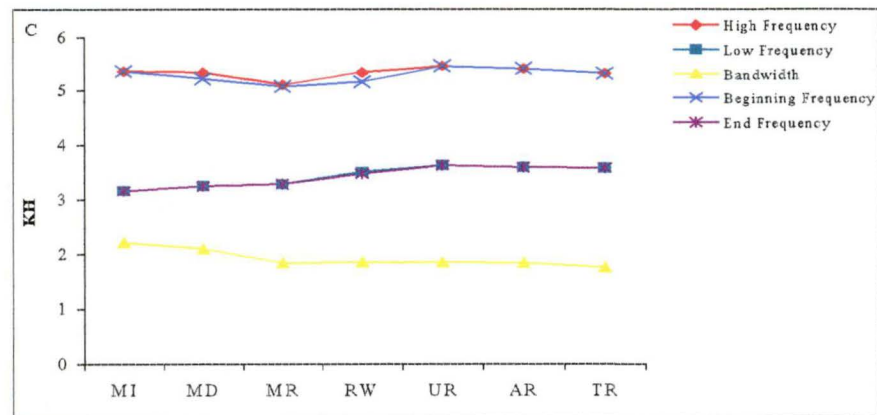
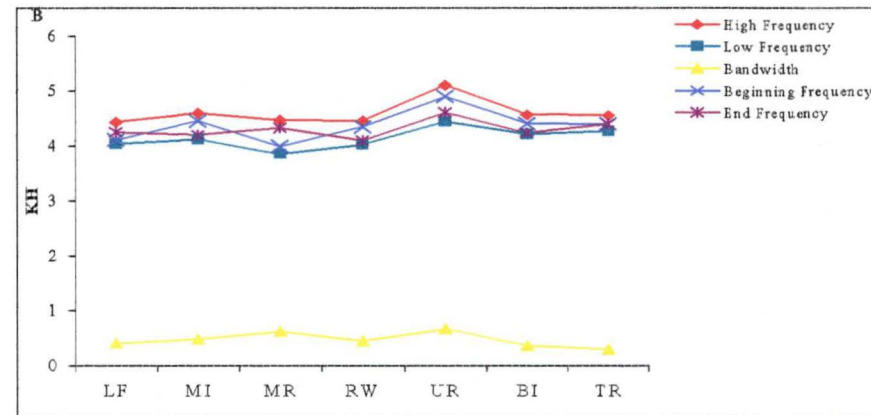
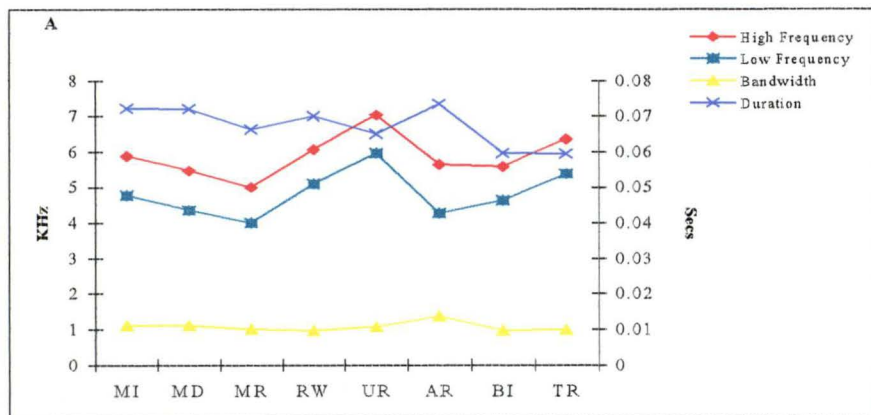


Figure 8.14 A-D show the variation in mean values for each parameter tested for syllables across geographic locations A is call type one, B call type two, C call type three and D call type four.

Table 8.3 Results of Bonferroni post hoc tests to determine where significant differences in syllable parameters lie. Sites are MI Maria Island, MR Meehan Ranges, MD Mount Direction, RW Ridgeway, UR University Reserve, AR Allens Rivulet, BI Bruny Island TR Tahune Reserve.

| | | High Frequency | | | | | | | | Low Frequency | | | | | | | | Bandwidth | | | | | | | |
|---|----|----------------|----|----|-------|-------|-------|-------|-------|---------------|----|----|-------|-------|-------|-------|-------|-----------|----|-------|-------|-------|-------|-------|-------|
| | | MI | MR | MD | RW | UR | AR | BI | TR | MI | MR | MD | RW | UR | AR | BI | TR | MI | MR | MD | RW | UR | AR | BI | TR |
| C a l l o n e | LF | | | | | | | | | | | | | | | | | | | | | | | | |
| | MI | | | | | 0.004 | | | 0.018 | | | | | <.001 | | 0.008 | <.001 | | | | | | 0.006 | | |
| | MR | | | | <.001 | <.001 | <.001 | <.001 | <.001 | | | | <.001 | | 0.002 | <.001 | <.001 | | | | | | <.001 | | |
| | MD | | | | | 0.001 | | | 0.016 | | | | | <.001 | | | <.001 | | | | | | | | |
| | RW | | | | | 0.031 | <.001 | <.001 | | | | | | | <.001 | <.001 | | | | | | | <.001 | | |
| | UR | | | | | | <.001 | <.001 | | | | | | | <.001 | <.001 | | | | | | | | | |
| | AR | | | | | | | | <.001 | | | | | | | <.001 | <.001 | | | | | | | <.001 | |
| | BI | | | | | | | | <.001 | | | | | | | | <.001 | | | | | | | | |
| | TR | | | | | | | | | | | | | | | | | | | | | | | | |
| C a l l t w o | LF | | | | | | | | | | | | | | 0.001 | | 0.04 | | | 0.007 | | 0.003 | | | |
| | MI | | | | <.001 | <.001 | | | | | | | 0.007 | | 0.001 | 0.004 | | | | | | | | <.001 | |
| | MR | | | | | <.001 | | | | | | | | | <.001 | | <.001 | | | | | 0.005 | | <.001 | 0.014 |
| | MD | | | | | | | | | | | | | | | | | | | | | | | | |
| | RW | | | | | <.001 | | 0.006 | | | | | | <.001 | | <.001 | | | | | | 0.003 | | 0.001 | |
| | UR | | | | | | | <.001 | 0.016 | | | | | | | | | | | | | | <.001 | 0.005 | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | TR | | | | | | | | | | | | | | | | | | | | | | | | |
| C a l l t h r e e | LF | | | | | | | | | | | | | | | | | | | | | | | | |
| | MI | | | | 0.006 | | | | | | | | | | | 0.014 | | 0.048 | | | 0.001 | | | | 0.031 |
| | MR | | | | <.001 | | 0.015 | | | | | | | | | | | | | | <.001 | | | | |
| | MD | | | | | | | | | | | | | | | 0.034 | | | | | | | | | |
| | RW | | | | | | | | | | | | | | | | | | | | | | | | |
| | UR | | | | | | | | | | | | | | | | | | | | | | | | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | TR | | | | | | | | | | | | | | | | | | | | | | | | |
| C a l l F o u r | LF | | | | | | | | | | | | | 0.037 | | | | | | | | 0.006 | | | |
| | MI | | | | | | | | | | | | | | | | | | | | | | | | |
| | MR | | | | | | | | | | | | | <.001 | | | | | | | | <.001 | 0.011 | | |
| | MD | | | | | | | | | | | | | <.001 | | | 0.002 | | | | | <.001 | | | |
| | RW | | | | | | | | | | | | | | | | | | | | | | | | |
| | UR | | | | | | | | | | | | | | | | | | | | | | | | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | TR | | | | | | | | | | | | | | | | | | | | | | | | |

Table 8.3 continued Bonferroni post hoc tests to determine where significant differences in syllable parameters lie.

| | | Beginning Frequency | | | | | | | | End frequency | | | | | | | | Duration | | | | | | | |
|---|----|---------------------|----|----|----|----|----|----|----|---------------|----|----|----|----|----|----|----|----------|----|----|----|----|----|----|----|
| | | MI | MR | MD | RW | UR | AR | BI | TR | MI | MR | MD | RW | UR | AR | BI | TR | MI | MR | MD | RW | UR | AR | BI | WR |
| C a l l o n e | LF | | | | | | | | | | | | | | | | | | | | | | | | |
| | MI | | | | | | | | | | | | | | | | | | | | | | | | |
| | MR | | | | | | | | | | | | | | | | | | | | | | | | |
| | MD | | | | | | | | | | | | | | | | | | | | | | | | |
| | RW | | | | | | | | | | | | | | | | | | | | | | | | |
| | UR | | | | | | | | | | | | | | | | | | | | | | | | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | TR | | | | | | | | | | | | | | | | | | | | | | | | |
| C a l l t w o | LF | | | | | | | | | | | | | | | | | | | | | | | | |
| | MI | | | | | | | | | | | | | | | | | | | | | | | | |
| | MR | | | | | | | | | | | | | | | | | | | | | | | | |
| | MD | | | | | | | | | | | | | | | | | | | | | | | | |
| | RW | | | | | | | | | | | | | | | | | | | | | | | | |
| | UR | | | | | | | | | | | | | | | | | | | | | | | | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | WR | | | | | | | | | | | | | | | | | | | | | | | | |
| C a l l t h r e e | LF | | | | | | | | | | | | | | | | | | | | | | | | |
| | MI | | | | | | | | | | | | | | | | | | | | | | | | |
| | MR | | | | | | | | | | | | | | | | | | | | | | | | |
| | MD | | | | | | | | | | | | | | | | | | | | | | | | |
| | RW | | | | | | | | | | | | | | | | | | | | | | | | |
| | UR | | | | | | | | | | | | | | | | | | | | | | | | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | WR | | | | | | | | | | | | | | | | | | | | | | | | |
| C a l l F o u r | LF | | | | | | | | | | | | | | | | | | | | | | | | |
| | MI | | | | | | | | | | | | | | | | | | | | | | | | |
| | MR | | | | | | | | | | | | | | | | | | | | | | | | |
| | MD | | | | | | | | | | | | | | | | | | | | | | | | |
| | RW | | | | | | | | | | | | | | | | | | | | | | | | |
| | UR | | | | | | | | | | | | | | | | | | | | | | | | |
| | AR | | | | | | | | | | | | | | | | | | | | | | | | |
| | BI | | | | | | | | | | | | | | | | | | | | | | | | |
| | WR | | | | | | | | | | | | | | | | | | | | | | | | |

8.4 Discussion

The first aim of this chapter was to describe, analyse and classify the vocalization of *M. affinis*. Four main calls, or basic call structures (Mundinger 1982) were identified and the behaviour associated with these calls considered.

Call type one typifies the response of the species to invasion or threat by interspecific species. The call is accompanied by individuals physically harassing the threat, either by perching or actively flying around the threat. This behaviour was typical of when the study species encountered *Dacelo novaeguineae* or *Colluricincla harmonica*. Generally the response from the intruding birds was nonchalant.

This call type is consistent with the description of terrestrial alarm calls as defined by Wood *et al.* 2000). These are calls that are loud, repeated pulses that cover a wide range of frequencies. These are properties that make the calls easy to locate. The behaviour of *M. affinis* with this call type is typical of terrestrial alarm calls, where the calling bird mobs or drives out intruding predatory birds (Wood *et al.* 2000). These calls also recruit other birds to assist in the displacement of a threat (Taylor *et al.* 1990).

The second basic call structure identified was that of the territorial breeding call. This call type is seasonal in use, only being recorded between late August to February, when birds are breeding. The call was most frequently recorded from male birds.

The use of breeding calls in analysis of animal calls is the method employed in many studies. Song is important in mate choice and male-male competition (O'Loughlen & Beecher 1999), and subsequently has led to the theoretical possibility that acoustic divergence in song could affect gene flow and divergence in populations (Ellers & Slabbekoorn 2003). However, passerines call all year and for species that show migratory (or nomadic tendencies), geographic relationships found in breeding calls may breakdown or become rearranged during non-breeding periods (Warren 2003).

Phrases in this call type of *M. affinis* vary in the repetition of syllables, though most commonly it was constructed of the quick repetition of notes within a

small frequency range (figure 8.5).

The similarities in the Bruny Island songs become apparent in the produced MDS plot. These songs, though overlapping with songs from other sites, group more closely together than the songs from other sites. One of the agreed influences on avian vocalizations is the importance of vocal tradition, where songs and syllables are passed on through family group and are thus socially learned (Mundinger 1982). This may account for the increased similarities, or less song variation, in the Bruny Island breeding songs. If these birds are relatively isolated from the mainland Tasmanian birds, then it would be expected that, without the input of songs from an outside source, these birds might retain only a small range of songs, passed on through family groups. This loss of acoustic variability in the Bruny Island birds (and possibly Maria Island birds), though only determined from small sample sizes, is archetypal of the trends encountered within other island populations. Commonly observed effects of population isolation is loss in variety in songs, with forms tending towards simplification (Baker *et al.* 2003). Sampling within locations may also play a role in the similarities seen in the Bruny Island songs as only a single sampling trip was undertaken and calls were recorded within a limited site.

Again significant variations were recorded within the syllables of this call type, with the most distinct differences being those calls recorded at University Reserve (6 figure 8.1). As with call type one, the frequency at which these syllables were expressed was significantly higher than other sites. Also, consistent with call type one, the calls recorded within the Meehan ranges spanned a lower frequency than other sites, again significantly so with some sites.

Call type three is a typical call of *M. affinis*, characteristically emitted as individuals take flight, and continued whilst in flight. The repetition of syllables in this call varies, but is generally emitted in multiples. Song classification across sites shows a wide overlap with limitations in the variation. There are however, four individual songs that appear distinctly different, and appear separated on the MDS plot. One of these songs is a Maria Island song, the other three recorded at Mount Direction. The

major difference for the Maria Island call is the starting frequency of the syllables within the song at 4.8 KHz, is lower compared to of other songs that begin at a frequency >5KHz. These anomalies may be described in one of two main ways – the songs are the result of isolation within the field sites where calls were recorded and have developed unique to that place or perhaps these sites have been more open to invaders which have brought new song types to the geographic location (Mundinger 1982) allowing for song changes to occur. This basic call shows the least variation in syllable parameters (see fig. 9.14C), with a general north/south trend occurring. The more northern sites tend to end at a lower frequency than the more southern sites, resulting in a decreasing band width with latitude. Syllables recorded at Ridgeway and Mount Direction do not begin on their maximum frequency as occurs at other sites, and, again, the syllables of Meehan Range calls show significantly lower maximum frequency than other sites.

The final basic call to be explored is that of the typical ‘squeaky’ contact call of the study species. This call is characterised by numerous frequency peaks and troughs, the number varying between sites. Of all the basic call types, this call has the potential to show the most variation between geographic sites due to the function of the call. It is a contact call between individuals within a flock (or family group), with generally low amplitude. As the calls are contained to flocks, potentially flock specific, the idea of tradition (Mundinger 1982) in call learning becomes more important.

These songs show much great spatial distribution across the MDS plot (fig. 9.13) than other call types, further indicating greater variation in the songs of *M. affinis*.

When looking at the syllable parameters, the most marked difference for this call type is the low frequency and beginning frequency. For both parameters (which are equal as this call begins on the lowest frequency) the calls from Mount Direction are significantly different from all other sites, showing changes within this contact call with location.

8.4.1 Call Frequencies

There is evidence indicating that the vocalizations of an avian species are strongly associated with the habitat in which the species exists (Morton 1975; Hunter & Krebs 1979; Keast 1993). In a study of the basic structural and acoustic features of 27 forest bird species, Keast (1993) found that Australian birds show vocalization characteristics common with forest birds elsewhere – 70% of the birds vocalizations were at frequencies between 1 – 5 KHz. This decrease in frequency is strongly correlated with the density of vegetation, with higher frequencies attenuating to a much greater extent under denser vegetative conditions, thus reducing the clarity of information being passed between individuals (Hunter & Krebs 1979).

Of the *M. affinis* calls analysed, only one basic call structure fell completely below the 5 KHz mark on the produced spectrographs, and thus within a low frequency as defined by Keast (1993). This was call type two; territorial/breeding calls. If the evidence presented by Morton (1975) and Hunter and Krebs (1979) is consistent within *M. affinis*, it is perhaps logical that the calls generated by individuals that are relevant to the population of *M. affinis* in an entire area, are transmitted at a frequency to produce maximum communication and maximum distance. These calls fall within the 4 - 5 KHz range, reducing the attenuation of calls across a site. The other necessary call to fall within this range is the alarm call (see figure 8.9) emitted in response to raptors or other potential threats, again a call type with a wide application within the entire bird community.

The three other basic call structures analysed breach this low frequency mark of 5 KHz, whether it be at the beginning of a syllable, end or frequency peak. These calls are more frequently used within a group situation, and over shorter distances, and subsequently the risk of attenuation is reduced. These birds generally interact in tight pairs/groups, and as such, the transmission of information within the group over long distances is not a general necessity, thus the impact of environmental constraints on contact calls are released, allowing for this increase in frequency.

In comparison to the honeyeater calls analysed by Keast (1993), the calls of *M. affinis* are seen to reach a higher frequency than other members of this

family. *Anthochaera chrysoptera* called in the range of 0.5 – 8.0 KHz, a range similar to *M. affinis* (1.7 – 8.8 KHz across all recorded calls), whilst *Meliphaga lewini* (1.6 – 2.9 KHz), *Lichenostomus chrysops* (1.0 – 4.3 KHz) and *Acanthorhynchus tenuirostris* (2.6 – 3.8 KHz) call in much narrower and lower frequencies. Comparing *Melithreptus affinis* to *M. lunatus*, again a higher frequency of calls is seen in the Tasmanian species. The spectrograms presented in HANZAB (2001) of alarm calls of *M. lunatus* place the frequency of these calls around the 2 KHz band. As seen in figure 8.9 of this chapter, similar functioning calls of *M. affinis* are at almost twice the frequency of its mainland counterpart. One other Tasmanian honeyeater species has had acoustic analysis of its calls (Bruce 1988a; Bruce 1988b). This was *L. flavicollis*, and frequency range was consistent with mainland records (Bruce 1988a, b; Keast 1993).

These differences may in part be due to the vegetation type and location in which the calls have been recorded. There is evidence to suggest that physical structure of habitat influences sound transmission (Liskens *et al.* 1976; Cosens & Falls 1984). Hunter & Krebs (1979) encountered a large amount of variation in the calls of *Parus major* across different forest and woodland types. In the more open woodland types the maximum frequency of calls increases. This may account for some of the variation between the Tasmanian calls and the mainland honeyeater comparisons, as *M. affinis*, is more prevalent, though not confined to, more open woodland types. Ecological difference, such as *M. affinis* being a foliage specialist, may also contribute to the differences in the frequencies utilised by this species. This change in vegetation may also account for some of the variation within the recorded call within southern Tasmania. The basic call structures of call one and two were both found to be significantly greater in maximum frequency in the University Reserve calls. This site is much more open than any other site, with large areas supporting a number of sporting fields. Subsequently the vegetation needed to cause the levels of attenuation within calls, and thus limiting frequencies, is not present. Urban noise may also be influencing the calls at this site. Slabbekoorn and Peet (2003) have found significant increases in the frequency of urban tits, in an effort to have their breeding calls heard over

the background noise. This may be an issue for the birds recorded at the University reserve as the “Southern Outlet”, the major arterial road out of Hobart to southern Tasmania, runs behind this site. Conversely to the University Reserve calls, calls from the Meehan ranges showed significantly lower maximums than other sites. Again, this may be reflective of the environmental conditions at this site. Though vegetation is no more dense than other sites, the location sampled for calls is a gully of 50-60m wide, with vegetated slopes. The difference in topography of this site, the narrow gully and wooded slopes may be enough to influence the frequencies of calls. This finding supports the Acoustic Adaptations hypothesis, that variation in bird song may result from the differences in acoustic properties of habitat (Doutrelant *et al.* 2001).

8.4.2 Geographic Variation and Dialect

The occurrence of divergence in animal signals between different populations is a recognised phenomena (Baker *et al.* 2000; Naguib *et al.* 2001; Warren 2001). Three main conditions influence the development of geographic variation, with a continuum between isolated dialects at one extreme, to no variation at all. These conditions are an isolation of population, a means of transmitting song from generation to generation and sources of variation by which localities may diverge (Field 1996).

Due to the high mobility of *M. affinis* during non-breeding periods, the degree of geographic variation in this species calls should be limited geographic group should mix during these periods. Across the geographic range sampled, the main songs analysed are found to occur across all sites, thus the classification as basic calls as defined by Mundinger (1982). These geographic ranges may be considered at either a macro scale – across a species range, or at a micro scale, which considers the variation of calls within a specific location. Looking at calls at these two scales, widely varying characteristics of song, social interactions and ecology are considered. Microgeographic variations tend to focus on the processes and results of cultural evolution, resulting in phonic variations. Macrogeographic variations tend to emphasize the effects and processes of biological evolutions, with

results in variation in syllable repertoire (Mundinger 1982). The calls of *M. affinis* are consistent with these definitions.

Phrase variations in the study species do not conclusively show macrogeographic effects, as there is considerable overlap in the call points determined by the MDS plots. This has been the typical method of determining geographic variation (Tracy & Baker 1999). These authors suggest that it may be more indicative of geographic influence to consider songs at a syllable level, depending upon the way in which a bird interprets the songs of another individual. Considering *M. affinis* songs at a syllable level, geographic variations begin to emerge, these appearing to be as biological effects (see above section on frequencies), consistent with Mundingers (1982) definitions.

Not only were the syllable parameters significantly varied with geographic distribution, but physical differences can be seen within the spectrograms for some call types. There are also apparent song types for some calls, distinctly separate from other geographic localities. On a macro scale, geographic effects can be seen in the four base calls analysed for *M. affinis* in this study.

The sample sizes of songs from localities were not numerous enough to consider microgeographic aspect of vocalizations of *M. affinis*. It is at this gradation of investigation that dialects begin to emerge within a species (Naguib *et al.* 2001). Dialects have been defined as a variant in song tradition shared by members of a local population of birds with boundaries delineating it from other variant song traditions (Mundinger 1982). For many species, dialects have been established (Miyasato & Baker 1999; Baker *et al.* 2000; Wright & Dorin 2001; Warren 2003;), whilst others show no dialect patterns at all (Bruce 1984; Tracy & Baker 1999; Nelson 1999), and songs are shared between populations such as in *Carpodacus mexicanus* (House Finch) (Tracy & Baker 1999). At the extreme end is *Lichenostomus flavicollis*, where no syllable pattern can be identified within the species (Bruce 1984).

In order to determine if dialect variations exist within the *M. affinis* population a much larger song sample would need to be taken within individual sites. Also a method of identification would need to be employed, a task found difficult in this species. There is evidence that micro-geographic variation

in song does occur when the MDS plot of call four and the function of this call are considered. Further investigation is necessary to conclusively determine if indeed these song differences are dialects.

8.5 Conclusion

Seven basic call structures were identified as occurring within the population of *M. affinis*. Of the call types defined, the most represented in records were described and analysed for geographic variation.

Call types showed different frequency bands, with contact calls, or short distance calls being vocalized at a higher frequency than those call types used to communicate across longer distances.

Call types were consistent across the geographic region where calls were samples, though variations in the parameters of *M. affinis* calls were encountered. Significant differences in frequency of calls were encountered between sites. This may be a response to the environment conditions of the individual sites, supporting the Acoustic Adaptations hypothesis (Doutrelant *et al.* 2001). Further work is needed to determine if dialects occur within this species.

9. GENERAL DISCUSSION

9.1 Synthesis

The main aim of this research was to study the ecology of a previously unstudied avian species. A small amount of literature has been available on *M. affinis*, but what this study has shown is there have been misrepresentation in regard to the biology of this species.

The Black-headed honeyeater, *M. affinis* is a woodland species, generally a canopy feeder, gleaning on the foliage of *Eucalyptus* species. *M. affinis* has the ability to vary foraging method as necessary depending on the environmental conditions or season. This is possibly in response to invertebrate availability, but until such data is available in Tasmania for invertebrate abundance this connection cannot be definitely established. Though feeding method changes from foliage gleaning to probing within the twigs and bark of eucalypts, the microhabitat in which the species is foraging does not change. The upper canopy is the preferred microhabitat. The species appears to behave consistently throughout the year, with breeding season not significantly changing the time budget in the species.

This study has shown the importance of White gum, *Eucalyptus viminalis* to *M. affinis* in the region. In both foraging and breeding, *E. viminalis* is selected significantly more frequently than other eucalypt species, even though it is not the dominant eucalypt in the floral assemblage (North 1998, 2000). *Eucalyptus pulchella* (Narrow-leaved Peppermint), the dominant eucalypt species in the floral assemblage, is a consistent, secondary resource, used during both good and poor seasons at the same rate.

When breeding, *M. affinis* selects larger, established eucalypts, nesting in the outer most branches. Nest are constructed in two ways, either suspended in the foliage or with twigs built into the rim providing support to the structure. The nest is larger than records for *Melithreptus lunatus*, the mainland congeneric of *M. affinis*. Other breeding traits are consistent with expectations for members of the Meliphagidae family. The only trait to show divergence from other Melithreptids is that of incubation period, which is

longer than would be expected.

Parental investment in *M. affinis* is consistent with other monogamous avian species. After the initial investment made by the breeding female in egg laying, both the male and female contribute to the raising of offspring. The workload associated with provisioning young appears to be evenly distributed. Feeding of offspring becomes more frequent as young age, but the amount of food provided (indirectly measured as the time period adults spend in attendance of young) significantly decreases as young mature - less food is provided more often.

Recording of the vocalizations of *M. affinis* found seven main call types. Four of these were described analysed. Call types were consistent across the geographic region sampled, though significant variation occurred between the measured parameters of the call types. It is hypothesized that these variations may be a response to the environmental conditions encountered at individual sites.

The secondary aim of this research was to determine if the vast body of literature available on island biogeography and avian adaptations to insular environments is applicable in this instance. Two major areas of this literature were considered – ecological and morphological variations, and breeding biology. The next section of this final discussion is committed to discussing these aspects of *M. affinis* in a biogeographical context, and determining if this theory, developed in the Northern Hemisphere can be supported.

9.2 Island Biogeography

9.2.1 Ecological and Morphological variations

Keast (1968b) and Abbott (1974) have concisely described the morphological variations displayed by *M. affinis*. *Melithreptus affinis* have a shorter bill (10% shorter) and shorter bill/wing ratio (8%), but longer tarsus (4%) and tarsus/wing ration compared to the mainland *M. lunatus* (Keast 1968b). There are also substantial differences in the hallux/tarsus ratio, with *M. affinis* showing a 60% ratio compared to 30-45% in the other members of the

genus (Keast 1968b). These features – short beak, short hallux – are specialized features, convergent with other foliage gleaning species (Keast 1968b). These morphological features may be considered more specialized than the mainland *M. lunatus*, the converse of island trends elsewhere, where insular (sub)species show more generalized traits than their mainland counterparts (Grant 1976, 1979).

The more specialized morphological traits of *M. affinis* are reflective of the foraging and diet of the species. Ridpath and Moreau (1966) state that the most abundant food resource utilized by birds in Tasmania are insects. This statement is strongly supported by the foraging observations taken during this study. Records of nectar consumption are negligible in the current study, and other studies of the foraging of *M. affinis* (Thomas 1980; Slater 1994) have limited, if any, record of nectar consumption. Studies of mainland Melithreptids have found nectar, though not the major food of the genus, does contribute a greater proportion to the diet than records for the Tasmanian species indicate. Ford (1979) calculated the percentage of observations of foraging at nectar sources for *M. lunatus*, *M. brevirostris* and *M. gularis*. These were 24%, 35% and 18% respectively. Ford and Paton (1977) also recorded a contribution of nectar to the diet of the same Melithreptid species. It was also noted that these short-beaked honeyeaters mainly fed on the open cup flowers of *Eucalyptus*. McFarland (1984) states that these foraging behaviours may result in insects being consumed rather than nectar, as the blossoms of *Eucalyptus* attract a high abundance of insects. The majority of observations of Melithreptids are of foraging in the leaves and bark. Recher (pers. comm.) believes the genus has more dietary dependence on alternate carbohydrates such as lerps rather than foraging on insects from the canopy. Woinarski *et al.* (1989) however, found *M. lunatus* consumed only a small percentage of lerps offered under experimental conditions, and *M. brevirostris* consumed both the lerp and the hemipteran nymph in approximately 60% of all observed feeding instances (Woinarski *et al.* 1989).

This study found *M. affinis* foraging in the foliage, though a large proportion of time (30-40%) was spent probing along trunks and within bark. This differed from other studies where almost 100% of observations were of

foliage use (Thomas 1980; Slater 1994). Also, although the species showed selection for upper canopy substrates, a large proportion of observations were taken in the mid-canopy. Mid canopy observations were more often of probing behaviours.

These results differ from the observations by other authors that this genus is an upper canopy specialist, specifically foraging within the foliage. A wider range of habitat and foraging substrates were utilised during the study period, consistent with the notion of ecological release (Sorensen 1997), an occurrence strongly associated with island avifauna (Grant 1976, 1979; Sorensen 1997). This may however simply be the response of *M. affinis* to periods of environmental stress. The rainfall data presented in this study shows that the study period was generally drier than the long-term averages for the study region would predict. This may in fact have driven the study species to utilize resources that it would not otherwise depend upon. In studies by Thomas (1980) and Slater (1994) gleaning is the dominant foraging behaviour, with Thomas recording almost all observations in the foliage. Slater (1994) recorded a wider range of foraging zones with foliage and branch/trunk zones showing equal distribution during the breeding period. Foraging behaviour will depend on the distribution of available resources. Optimal behaviour will vary spatially and temporally as the amount and distribution of food varies (Thomas 1980). Thus the results of habitat use and time budget in this study may not be consistently displayed by the study species. The apparent widening of foraging substrate and habitat may be a response to the environmental conditions of the time and not be a result of ecological release. *Melithreptus affinis* shows much more specific morphological adaptations than other members of the genus, suggesting a more specific foraging strategy. A smaller beak limits prey size (Saunders *et al.* 1995), method of capturing prey (Grant 1979), and foraging substrate (Grapputo *et al.* 1998) selected by birds. The foot and leg morphology are typical of small, foliage gleaning birds (Keast 1968b; Zeffner *et al.* 2003), again limiting the foraging substrate of the species. This is converse to the island literature where (sub)species show more generalised traits and a widening of niche (Grant 1965, 1976, 1979). Tasmania supports a

depauperate avian assemblage (Thomas 1974), which should allow for species to broaden niches. There appears to be a shift in the niche of *M. affinis* to that similar to the foliage gleaners of mainland Australia not found in Tasmania.

9.2.2 Breeding variations

The list of characteristics developing in insular species in relation to their breeding strategies do not appear applicable in *M. affinis* and its allopatric mainland species *M. lunatus*. The results of this study show that *M. affinis* does not show a decrease in clutch size does not show increased nestling development and reproductive success in the study species falls approximately midway between mainland extremes in the Meliphagidae family (see table 6.7). This is converse to island avifauna in the Northern Hemisphere where reproductive traits show distinct differences within insular populations (Cody 1966; Higuchi & Momose 1981; Higuchi 1976; Wiggins *et al.* 1998). The only difference encountered in *M. affinis* is the length of incubation period. Subsequently, these aspects of the literature for Northern Hemisphere avifauna are not applicable in this context. This is not surprising when it may be considered that the entire continent is considered an island (Lack 1976), with general reproduction within Australian endemic families displaying characteristics consistent with insular species in the Northern Hemisphere counterparts (Woinarski 1985a; Yom-Tov 1987). Add to this the suggestion that the Tasmanian endemic avifauna may have colonised the landmass before Bass Strait receded, rather than afterwards (Abbott 1973), then one would not expect differences in the island species, as they may be considered continental.

9.2.3 Continental versus Island species

As outlined above, *M. affinis* does not exhibit any of the characteristics attributed to island environments in Northern Hemisphere avifauna. There appears to have been a shift in the foraging niche of *M. affinis*, but not an expansion, and there are no variations in breeding behaviour consistent with

island avifauna elsewhere. The one characteristic of breeding that does differ in *M. affinis* is one that would be detrimental to a species invading an environment because it would reduce population growth rate (Duncan *et al.* 2001).

This can be interpreted in a number of ways. Firstly the island biogeographic literature may not be applicable in a Tasmanian, and potentially the Australian context. This would be a very controversial statement, which needs much more research to substantiate. Also, a small amount of evidence on non-endemic species in Tasmania is in line with literature in other areas. The Grey Shrike-thrush *Colluricincla harmonica* has evolved a bill much larger than mainland birds, and has shifted its foraging niche to use bark more than mainland counterparts (Keast 1970; Thomas 1978). The Brown thornbill *Acanthiza pusilla* shows a striking case of ecological versatility, foraging significantly more in the canopy in Tasmania than encountered in mainland habitats. This species also forages extensively on trunks and branches, using foraging zones that are filled by other *Acanthiza* sp. on the mainland (Keast 1970).

Another interpretation is that it is *M. affinis* that does not fit with the literature. If this is the case, the question raised is why? I consider that this may be attributed to the history of *M. affinis* on the Tasmanian mainland, with it having a longer history than previously supposed, allowing it to be considered a continental species, rather than island species.

I believe that more evidence has come to light during this study to support the idea that aspects of Tasmania's avifauna have a longer history on the island, dating back to before the island was finally separated from mainland Australia. Ridpath and Moreau (1966) found ecological evidence to conclude that the Scrubtit *Sericornis magnus* has invaded Tasmania and survived the glacial conditions, fossil evidence confirms that modern species were extant during the final glacial maximum and lifehistory traits encountered during this study do not support the notion that all modern avifauna invaded Tasmania as the Bass Strait landbridge was closing for a final time. The most suggestive of these is the extended incubation period in the study species compared to

other honeyeater species.

There is a known relationship between the length of a species' incubation period and weight of adult, as well as egg volume (Ricklefs 1993). Simply stated, the larger an avian species, the greater the egg volume. This results in a longer incubation period. Simple linear regression will support this relationship. Figures 9.1 and 9.2 present this relationship for the Australian Meliphagids presented in table 6.6.

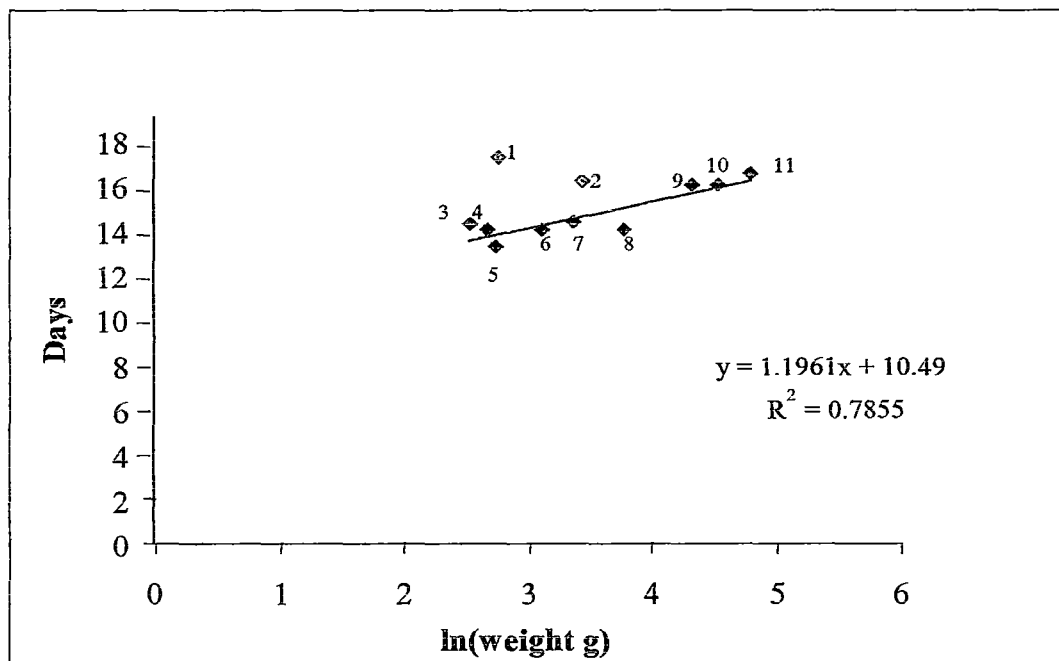


Figure 9.1 Regression relationship between the natural log of Australian Meliphagid's weight (grams) and length of incubation (days). Points 1 and 2 (red, Tasmanian species) not included in the regression line. Numbers are allocated to species as follows: 1 *Melithreptus affinis*, 2 *Lichenostomus flavicollis*, 3 *Conopophila albogularis* 4 *M. lunatus*, 5 *Phylidonyris pyrrhoptera*, 6 *P. novaehollandiae*, 7 *Manorina melanophrys*, 8 *Xanthomyza phrygiai*, 9 *M. melanocephala*, 10 *Philamon corniculatus* and 11 *Anthochaera carunculata* (Source of data as of table 6.6)

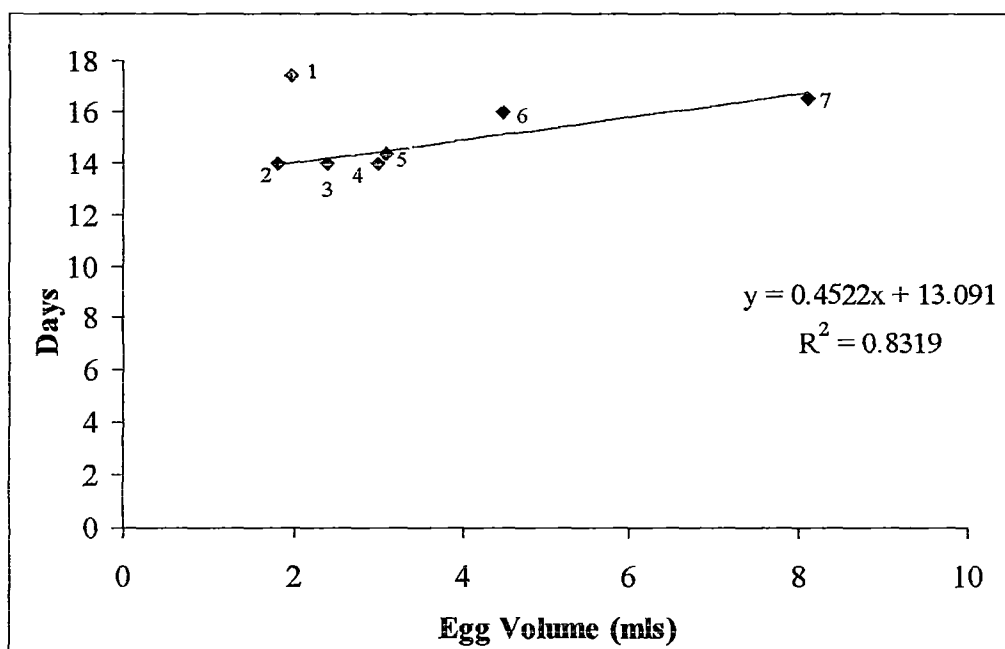


Figure 9.2 Regression relationship between Egg Volume (mls) and incubation length (days) for Australian members of the Meliphagid family. Point 1 in red (Tasmanian species) not included in regression line. Species are as follows: 1 *Melithreptus affinis*, 2 *M. lunatus*, 3 *Phylidonyris novaehollandiae*, 4 *Lichenostomus melanops*, 5 *Manorina melanophrys*, 6 *M. melanocephala* and 7 *Anthochaera carunculata*. (Source of data Poiani & Jermin 1994)

Both these relationships are significant at a 95% level. Significance values and confidence intervals are presented in table 9.1.

Table 9.1 Significance values and confidence interval for members of Australian Meliphagidae.

| | F value | Significance | Upper 95% | Lower 95% |
|---------------------|---------|--------------|----------------------|---------------------|
| Egg Volume (mls) | 14.432 | 0.032 | 14.8364 (±0.0825) | 11.407 (± 0.073) |
| ln Weight (g) | 9.56 | 0.021 | 13.766 (± 1.99) | 7.641 (± 0.231) |

For both these regressions the addition of *M. affinis* (and *L. flavicolis* in weight regression) cause the models to become non-significant. The measured incubation period for *M. affinis* is much greater than the predicted period (17.67 days actual compared to 13.81 using weight and 13.95 using egg volume). The actual incubation period falls outside of the confidence interval calculated by the model, further contributing to the evidence that this life history trait is very unusual in *M. affinis*. Considering this aspect with regards to another endemic Tasmanian honeyeater, *Lichenostomus flavicolis*, the incubation period of this species (Bruce 1988) is also longer than that which would be predicted with the regression model. For other species of honeyeater in Tasmania, there is only primary research available on one other species – *Phylidonyris novaehollandiae*. This species does not exhibit changes in incubation (or other breeding traits, Yuni 2002) compared with studies conducted on the mainland. Whether this trend is consistent in the other two endemic honeyeaters or other endemic passerines is an area for future research. At this stage there are no primary sources, or research on either *Melithreptus validirostris* or *Anthochaera paradoxa*, so whether this characteristic extends to these honeyeater species is unknown.

How does this characteristic of extension in incubation relate to the history of the species in Tasmania? It may be a latitudinal affect, but latitude does not appear to impact upon this aspect of avian biology, though there is continuing support for clutch size variation with latitude (Cardillo 2002). The other possibility is that it is an adaptation to a cold climate, perhaps remnant behaviour from glacial conditions. The characteristic of incubation can relate to the invasiveness of a species. A species that has high invasive potential has a relatively short incubation period. This allows for a high population growth rate (Duncan *et al.* 2001), thus reducing the chances of extinction. It is suggested that in the case of *M. affinis*, if it has invaded Tasmania after the island became isolated, it would not have been able to compete with other species with a shorter incubation period and so faster population growth rate. Subsequently, *M. affinis* should not have been able to populate the island to the extent that it has with this reduction in potential

population growth. This, combined with the level of reproductive success calculated for the species (31% - see chapter 6), implies that this species would not be successful in colonizing an isolated environment if in competition with more species or species with a life history more conducive to invasion.

Chapter one of this thesis reanalyses the invasion of Tasmanian avifauna in the context of modern paleobotanical and climatic evidence. What this has shown is that necessary habitat was probably available in Tasmanian during the glacial periods in protected valleys and coastal regions, providing respite from the climatic conditions for not only the flora. The botanical evidence also suggests that woodland birds may have moved across the Bass Strait landbridge as it developed rather than as it receded, as a result of the vegetational changes across much of the continent.

These environmental conditions, coupled with the morphological and breeding adaptations may indicate a longer history of *M. affinis* on the Tasmanian landmass than previously suggested (since the end of the last glaciation, Ridpath & Moreau 1966; Keast 1970). This bird species shows specialized morphology, shows dependence on a *Eucalyptus* species similar to another highly specialized, endemic species (*Pardalotus quadragintus*) and demonstrates a breeding trait that would not have been conducive to invasion and rapid population growth. These factors suggest to the author that *M. affinis* invaded the Tasmanian mainland (and islands) before other non-endemic species – either entering Tasmania during the penultimate glacial period and establishing itself during the last interglacial, or invading early in the final glacial period. It would be interesting to determine the time period when *M. affinis* differentiated from other members of the genus, as well as similar information for eucalypt species. Of most interest is *Eucalyptus viminalis* and the other white gums that support *P. quadragintus* and *M. affinis*.

Results from this study, that do not support the literature on insular avifauna allows the conclusion to be drawn that *M. affinis* should be considered a continental species rather than an island species, even though it inhabits an

island environment.

9.3 Study Limitations

Three major limiting factors were experienced during this study.

The first of these is simply the nature of the species. It is not an easy subject to study for the following reasons:

- It is nomadic during the non-breeding season. This made locating individuals difficult for time budget data, limiting the size of the data set for this section. It also resulted in long hours of field work with limited results as a consequence;
- The species is a canopy specialist, and not strongly aggressive limiting the success in banding efforts. This in turn limited what could be extrapolated from behavioural and nest observations.
- The species selects nesting sites for which direct access is very difficult. The height, and the distance from the stronger, central branches would make it unsafe to try to directly contact nests without appropriate training and equipment.

The second major limiting factor were the weather conditions during the three-year study period. Reduction in rainfall directly or indirectly affects the biota of an area. This is believed to have limited the breeding attempts of this species for two of the three breeding periods. Subsequently a larger data set on nesting biology could not be collated. This also had repercussions for the data collected for parental investment as the methodology was set during the first breeding season before it became apparent that breeding would be limited across the study period.

The final major limitation is the scarcity of primary scientific research on not only the study species, but Tasmania's avifauna in general. This has made drawing comparisons and determining what may be a result of the environment difficult as there is such paucity of literature available to compare with.

9.4 Conservation and Further Research

As with much ecological research undertaken today, conservation issues are at a forefront. Endemic species are of interest because of their conservation value – narrowly endemic species are by definition rare, and therefore potentially threatened (Crisp 2001). Though not a threatened species across its range, there is some anecdotal evidence that *M. affinis* has decreased in abundance across study sites during this study. This may be a result of the drier conditions and subsequent limited breeding (and recruitment) that has occurred over the past three breeding seasons. Coupled with this is an increase in the number of introduced species such as Starlings (*Sturnus vulgaris*) at the Ridgeway sites (Pers. ob).

The main threatening process to the species is that of habitat loss- the major threat to avifauna across the continent (Olsen *et al.* 2003). In Tasmania, *M. affinis* utilises woodland that is considered to be of economic value, and subsequently this vegetation may continue to be removed. To date, 88% of Tasmania's grassy woodlands have been cleared for agricultural purposes (Yates & Hobbs 1997). Table 9.2 provides estimates of the total pre-European area of woodland, the remaining percentage and how much is currently reserved. These values are taken from Mendel and Kirkpatrick (2002). Though this does not include all woodland types across which *M. affinis* is potentially found, the trends are obvious, and the impacts of habitat reduction and fragmentation effects on the species must be considered. Already the effects of wide scale landscape clearing have impacted upon the species on King Island. In 1925 Sharland listed *M. affinis* as highly abundant. By 1971 Green and McGarvie considered the species rare on the island. By 1985 (Fletcher 1985 ABBBS records) the species was still present on the island though numbers were minimal (Fletcher pers. com). This is not surprising if the remnant woodland on King Island is explored. Pre-European coverage of *Eucalyptus globulus*, *E. brookeriana*, *E. viminalis* wet forest on King Island totalled 152,800 ha. (Mendel & Kirkpatrick 2002). As of 2002 only 2% of this vegetation remained, with 0.5% of this pre-European area

reserved as of 2000 (Mendel & Kirkpatrick 2002). This is an extreme example of land clearance, but the long term effects on *M. affinis* are obvious and should be considered in the future of the species on the mainland of Tasmania. There is the possibility that the species is already locally endangered, but as no long term study has been undertaken on the species this will never be known. The mainland *M. gularis gularis* has already been scheduled as vulnerable within the NSW Threatened Species Act (1995), and is considered to be locally endangered across the Flinders Rangers (Chapman 1995).

Table 9.2 Relevant remnant vegetation in Tasmania, showing pre-European areas, percent remaining of this vegetation and how much of this remaining vegetation was reserved in Tasmanian as of 2000. Data from Mendel and Kirkpatrick (2002)

| Vegetation Type | Pre-European area (ha) | % Pre-European remaining | % Reserved 2000 |
|---|-------------------------------|---------------------------------|------------------------|
| <i>Eucalyptus viminalis</i> , <i>E. ovata</i> , <i>E. amygdalina</i> , <i>E. obliqua</i> (damp) | 80, 000 | 50 | 14.7 |
| <i>E. pulchella</i> , <i>E. viminalis</i> , <i>E. globulus</i> | 227, 200 | 67 | 18.4 |
| <i>E. viminalis</i> (grassy woodland) | 223, 900 | 49 | 1.2 |
| <i>E. viminalis</i> + or – <i>E. globulus</i> (coastal) | 7600 | 17 | 3.7 |

The results of this study indicate just how limited the ecological information is with regard to not only *M. affinis*, but also the entirety of Tasmania's terrestrial bird life. Simple baseline studies need to be undertaken on all species, but perhaps of most value are those of the other endemic species. Do they show variations in their breeding and foraging in comparison to mainland species, or do they, as with *M. affinis* show no difference that can be significantly attributed to isolation or other insular effects? Is the incubation period in other Tasmanian endemics also extended compared to mainland species, and if so why? These questions can also be applied to those species not endemic. Yuni (2002) in a study on the New Holland Honeyeater (*Phylidonyris novaehollandiae*) found that foraging and the breeding behaviour did not significantly differ from studies carried out on the

Australian mainland. If this is consistent within other species it raises questions to the applicability of island biogeography literature in regard to Tasmania's avifauna.

Specifically to *M. affinis* this study raises further questions to the social organization of the species. Movement patterns and non-breeding activities are highlighted. Of particular interest to the author is the movement between 'isolated' populations on Maria Island and Bruny Island and the mainland. Is there overlap, or are the island populations' genetic isolates? Vocal analysis does not show substantial variation in vocal parameters. If dialect was found to differ, this may indicate isolation of island populations.

General environmental questions are also raised. The importance of *E. viminalis* to this species parallels that of the Forty-spotted Pardalotes (*Pardalotus quadragintus*). Woinarski and Bulman (1985) indicate that this species of Eucalypt supports a higher abundance of lerp than other eucalypts. If this is so, what is the importance of this eucalypt species to, not only *M. affinis*, but other organisms in this woodland type?

This study has been a first step towards filling a large hole in the Tasmanian and Australian avian research. It has highlighted the unique adaptations of *Melithreptus affinis* to the environment that it inhabits and raised questions as to the validity of Northern Hemisphere theory in a Southern Hemisphere context (Ford 1989). Hopefully this study, and subsequent publications will promote research into other aspects of Tasmania's terrestrial avifauna.

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APPENDIX 1 List of Banding location, period of banding, number of birds banded and bander. This data was supplied by the ABBBS (2001).

| Site | Period of study | Number birds | Bander | Co-ordinates |
|--------------------------|-----------------------|--------------|------------------|---------------------|
| Exeter | 1965-70 | 16 | Green | 41°11' 146° 58' |
| King Island | 1984, 1989 | 3 | Harris; Fletcher | 39° 57' 143° 54' |
| Finders Island | 1985 | 4 | Lane; Fletcher | 39°59' 148°12' |
| Eugenana | 1989 | 3 | Sutton | 41° 13' 146°17' |
| Legana | 1987 | 1 | Henderson | 41°22' 147°2' |
| Port Sorrell | 1977 | 2 | Harris | 41° 18' 146° 37' |
| Maggs Mountain | 1983-90, 1992 | 307 | Green | 41°40' 146°12' |
| Little Chinaman's Bay | 1984 | 3 | Harris | 42° 56' 147° 53' |
| Mathinna | 1977 | 3 | Harris | 41° 24' 147° 59' |
| Waddamana | 1981, 1982 | 4 | Harris | 42° 8' 146° 44' |
| Clifton Beach/Goat Bluff | 1983-84 1985-87, 1989 | 40 | Harris; Fletcher | 42° 59' 147° 29' |
| Fortescue Bay | 1986 | 1 | Rose | 43°9' 147°58' |
| Lauderdale | 1984-86 | 17 | Blaber | 43°1' 147°31' |
| Leenah Valley | 1975, 1986 | 3 | Harris; Newman | 42°56' 147°15' |
| Meenah Ranges | 1986-89 | 73 | Fletcher | 42° 50' 147° 24' |
| Moonah | 1987 | 2 | Newman | 42°52' 147°16' |
| Pottery Road | 1986 | 2 | Newman | 42°52' 147°16' |
| Mount Nelson | 1973-75 | 29 | Harris | 42° 55' 147° 19' |
| Dysart | 1983 | 2 | Harris | 42° 35' 147° 15' |
| Ridgeway | 1975-85 | 108 | Harris | 42°56' 147°17' |
| The Lea | 1973, 1984 | 13 | Harris | 42° 56' 147°19' |
| Tinderbox | 1972, 1980-81 | 51 | Milledge; Harris | 43°3' 147°20' |
| Woodsdale | 1976 | 2 | More | 42° 30' 147° 40' |
| Maria Island | 1980 | 61 | Harris | 42° 37' 148° 3' |

APPENDIX 2 Data analysis of time budget method

Real time observations were calculated by dividing the time allocated to each behaviour classification by the total time of an observation. This resulted in a value representative of the proportion of time allocated to each behaviour.

With instantaneous sampling techniques, a total was calculated of the occurrence of each behaviour for each observation period. This was divided by the total number of behaviours records for each observation period, again providing a proportional value.

As data was proportional it was Arcsin transformed using the Freeman and Tukey equation (Freeman & Tuckey 1950 cited in Zarr 1999) (see chapter 2 section 2.5)

A total of 389 individual observations were used for analysis. Six of the nine behavioural classes were analysed statistically across methods. These were: glean, probe, fly, perch, preen, and inter/intraspecific interactions. These behaviours were selected as they were recorded in >20 of the observations. A coarse level analysis was also carried out on three grouping of the above behaviours. These were Feed, compiled of all records of glean, nectar and probe, Still, observations of perch or preen (individual is remaining sedentary) and Move, compiled from flight, inter/intraspecific interaction and move observations. Hawk was also included in the Move category as it was difficult to tell if all hawking incidents resulted in a definite feed, but it is an obvious movement by the bird.

Transformed data was explored for univariate (Lilliefors Statistics) and multivariate normality (Mahalanobis distance) and found not to violate necessary assumptions. Subsequently, a Multivariate Analysis of Variance (MANOVA) (see section 2.5 for details) was applied to determine if significance occurred between the three methods in the proportion of time allocated to behaviours.

What this analysis shows is that there are significant differences in the estimates of time allocation between the method types (fig 1). Assuming realtime measurements are the true proportion of time allocated to

differing behaviours, the measurements obtained using instantaneous sampling both over and underestimate behaviours. Common behaviours of extended duration are not impacted by method choice. Other behavioural types, such as both extended and short-term uncommon behaviours and common short lived behaviours, are incorrectly estimated by instantaneous sampling.

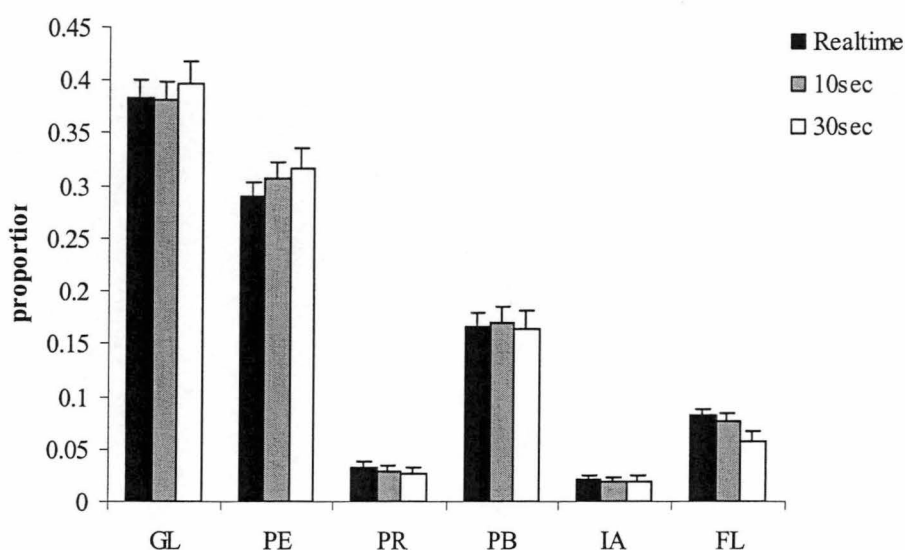


Figure 1 Comparison of proportional estimates of time allocated across three method types. GL Glean, PE Perch, PR Preen, PB Probe, IA Inter/intraspecific associations, FL Fly.

For the data set analysed, five of the six behaviours showed significant variation in the calculated proportion of time allocated to the behaviour (table 1). Glean was the only behaviour not be significantly vary with method. This is a long-lived, common behaviour in the study species, and thus the time constraints involved in instantaneous sampling should not affect the outcome. This behaviour would be frequently recorded, encompassing numerous sampling points across the observation period.

Table 1 Significant values for comparison of method types across behaviours.

| | Chi squared | d. f. | Significance value |
|-------------|--------------------|--------------|---------------------------|
| PE | 7.031 | 2 | P=0.001 |
| PR | 202.259 | 2 | p<0.001 |
| PB | 18.168 | 2 | p<0.001 |
| IA | 278.156 | 2 | p<0.001 |
| FL | 78.852 | 2 | p<0.001 |
| Move | 22.388 | 2 | p<0.001 |

Flight comparatively, is a high frequency behaviour, but of short duration. Subsequently it would fall between the sampling points more repeatedly, and subsequently be underestimated using instantaneous methods, as is obvious in figure 2.2.

Combining these behavioural groups at a coarser scale, only the time spent moving showed significant variation with method. For this grouping, there were significant differences between the realtime and instantaneous techniques. The 10sec and 30 sec intervals did not show significant variation.

What these results show is that the researcher must be clear on the questions being asked by their study, and determine if a frequency of behaviour is appropriate compared to the actual time spent demonstrating behavioural classification. What this also suggests is that studies using different methods not directly comparable, and again this should be considered during project design.

APPENDIX 3 SUMMARY TABLES OF AVERAGE VALUES USED IN STATISTICAL TESTS IN CALL ANALYSES OF *M. AFFINIS*.

Summary table of statistics for *Call type one* - grand means calculated. Site number corresponds to figure 9.1. 1 Lake Leake; 2 Lost Falls Reserve; 3 Maria Island; 4 Mount Direction; 5 Meehan Ranges; 6 Ridgeway (and University Reserve); 7 Allens Rivulet; 8 Bruny Island (South Island); 9 Tahune Forest Reserve. Site 6a is University Reserve. Value in brackets is the number of syllables measured for each site.

| Site | High Frequency (KHz) | Low Frequency (KHz) | Bandwidth (KHz) | Harmonics above | Harmonics below |
|-----------|----------------------|---------------------|-----------------|-----------------|-----------------|
| 3 (n=24) | 5.89± .142 | 4.77± .128 | 1.11± .056 | 0 (0, 1) | 1 (0, 1) |
| 4 (n=3) | 5.47± .444 | 4.35± .182 | 1.11± .264 | 1 (0, 1) | 1 (0, 1) |
| 5(n= 92) | 5.00± .04 | 4.00± .053 | 1.00± .029 | 2 (0, 6) | 1 (0, 3) |
| 6 (n=41) | 6.07± .093 | 5.09± .092 | .977± .033 | 1 (0, 2) | 1 (0, 1) |
| 6a (n=2) | 7.03± .001 | 5.96± .039 | 1.07± .040 | 1 | 0 |
| 7 (n=312) | 5.64± .016 | 4.27± .018 | 1.36± .019 | 1 (0, 2) | 0 (0, 2) |
| 8 (n=49) | 5.59± .088 | 4.63± .095 | .960± .046 | 0 (0, 2) | 1 (0, 1) |
| 9 (n=13) | 6.36± .091 | 5.37± .108 | .987± .132 | 0 (0, 1) | 1 (0, 1) |

Summary table of statistics for *Call type two* - grand means calculated. Site number corresponds to figure 9.1. 1 Lake Leake; 2 Lost Falls Reserve; 3 Maria Island; 4 Mount Direction; 5 Meehan Ranges; 6 Ridgeway (and University Reserve); 7 Allens Rivulet; 8 Bruny Island (South Island); 9 Tahune Forest Reserve. Site 6a is University Reserve. Value in brackets is the number of syllables measured for each site.

| Sites | High Frequency (KHz) | Low Frequency (KHz) | Bandwidth (KHz) | Beginning Frequency (KHz) | End Frequency (KHz) |
|-----------|----------------------|---------------------|-----------------|---------------------------|---------------------|
| 2 (n= 11) | 4.43± .065 | 4.03± .064 | .396± .023 | 4.12± .107 | 4.24± .065 |
| 3 (n= 46) | 4.59± .039 | 4.11± .025 | .476± .021 | 4.44± .029 | 4.19± .0317 |
| 5 (n= 6) | 4.46± .057 | 3.58± .094 | .613± .076 | 3.99± .172 | 4.32± .088 |
| 6 (n=147) | 4.44± .013 | 4.02± .013 | .433± .009 | 4.35± .015 | 4.09± .027 |
| 6a (n=4) | 5.10± .014 | 4.44± .040 | .660± .033 | 4.90± .095 | 4.61± .240 |
| 8 (n=48) | 4.56± .026 | 4.21± .021 | .354± .018 | 4.40± .025 | 4.23± .025 |

| | | | | | |
|---------|------------|------------|---------|------------|------------|
| 9 (n=2) | 4.55± .286 | 4.26± .202 | .285± 0 | 4.39± .134 | 4.39± .210 |
|---------|------------|------------|---------|------------|------------|

Summary table of statistics for *Call type three* - grand means calculated. Site number corresponds to figure 9.1. 1 Lake Leake; 2 Lost Falls Reserve; 3 Maria Island; 4 Mount Direction; 5 Meehan Ranges; 6 Ridgeway (and University Reserve); 7 Allens Rivulet; 8 Bruny Island (South Island); 9 Tahune Forest Reserve. Site 6a is University Reserve. Value in brackets is the number of syllables measured for each site.

| Sites | High Frequency (KHz) | Low Frequency (KHz) | Bandwidth (KHz) | Beginning Frequency (KHz) | End Frequency (KHz) |
|-----------|----------------------|---------------------|-----------------|---------------------------|---------------------|
| 3 (n= 16) | 5.37± .101 | 3.16± .077 | 2.21± .078 | 5.37± .101 | 3.16± .077 |
| 4 (n= 65) | 5.34± .033 | 3.25± .046 | 2.09± .046 | 5.22± .036 | 3.26± .046 |
| 5 (n= 61) | 5.11± .027 | 3.72± .032 | 1.83± .034 | 5.08± .027 | 3.27± .032 |
| 6 (n=5) | 5.34± .037 | 3.49± .047 | 1.85± .022 | 5.16± .219 | 3.62± .109 |
| 6a (n=3) | 5.46± .048 | 3.62± .109 | 1.84± .156 | 5.47± .047 | 3.62± .109 |
| 9 (n=7) | 5.33± .095 | 3.57± .055 | 1.76± .133 | 5.33± .095 | 3.57± .055 |

Summary table of statistics for *Call type four* - grand means calculated. Site number corresponds to figure 9.1. 1 Lake Leake; 2 Lost Falls Reserve; 3 Maria Island; 4 Mount Direction; 5 Meehan Ranges; 6 Ridgeway (and University Reserve); 7 Allens Rivulet; 8 Bruny Island (South Island); 9 Tahune Forest Reserve. Value in brackets is the number of syllables measured for each site.

| Sites | High Frequency (KHz) | Low Frequency (KHz) | Bandwidth (KHz) | Beginning Frequency (KHz) | End Frequency (KHz) |
|-----------|----------------------|---------------------|-----------------|---------------------------|---------------------|
| 2 (n= 5) | 5.26± .026 | 4.34± .112 | .918± .095 | 4.34± .112 | 5.10± .083 |
| 4 (n= 69) | 5.31± .136 | 3.23± .099 | 2.08± .102 | 3.23± .101 | 4.81± .115 |
| 5 (n= 28) | 5.17± .067 | 4.32± .093 | .857± .060 | 4.47± .091 | 4.97± .108 |
| 6 (n=51) | 5.54± .122 | 4.12± .127 | 1.41± .102 | 4.16± .131 | 5.17± .090 |
| 8 (n=9) | 5.73± .404 | 4.28± .402 | 1.45± .234 | 4.64± .525 | 4.89± .375 |